HOST PREFERENCE IN CIID BEETLES (COLEOPTERA: CIIDAE) INHABITING THE FRUITING BODIES OF BASIDIOMYCETES IN NORTH AMERICA

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CONTENTS

Abstract. Host records are summarized for 74 species of North American ciid beetles occurring in the fruiting bodies of 117 species of basidiomycete fungi, and the data are analyzed to determine patterns of host preference. The morphology and classification of the host fungi are reviewed and the life history and ecological role of the Ciidae are discussed. For species with five or more breeding records, an attempt is made to determine degree of host specificity, using a modified equation for "niche breadth." Few North American ciids are monophagous and probably none are indiscriminate, but most appear to be group-specific, preferring to breed in one or two hosts but occurring in several more, which are often phylogenetically related. The majority of host fungi may be placed into one of four host preference groups, on the basis of shared ciid inhabitants. These groups and their associated Ciidae are not mutually exclusive, but, with the exception of a few eurytrophic species, the beetles rarely breed in fungi of the "wrong" group. Each host preference group is discussed with respect to its faunal composition in each of four major geographical regions of North America. Speculations are made on the possible mechanisms of host selection, and certain zoogeographical and evolutionary factors are discussed.

INTRODUCTION

Beetles of the family Ciidae are the most common, if not the most conspicuous, arthropods inhabiting the relatively large and often woody or leathery fruiting bodies of the Polyporaceae and related higher fungi. Within this habitat, the Ciidae are represented by many more species than other inhabitants, such as tenebrionid beetles or tineid moths, and, although the individual size is small (usually 1 to 3 mm), the large populations constitute a major portion of the consumer biomass and contribute significantly to the breakdown of fungus conks (Matthewman and Pielou, 1971). This paper deals with patterns of host preference in 74 species of American Ciidae occurring north of the Mexican border, and is based on over 2000 host records gathered by myself and various colleagues.

Previous works on the inhabitants of fungi vary in scope and approach, and fall into four major categories: a) general compilations of host data for all organisms (or one large group) recorded from fungi within a certain geographic area; b) more detailed studies of one family or genus of fungus feeders, with an emphasis on host specificity; c) faunal analyses of a single host species; and, d) biological studies involving a single mycetophagous organism.

In the first category belongs the work of Benick (1952), which covers all beetles known from fungi in the Palaearctic region and includes 1116 species from 286 different hosts. Other more restricted studies include Donisthorpe (1935) [beetles, England]; Graves (1960) [all inhabitants, Chicago area]; Graves and Graves (1966 and in preparation) [all inhabitants, North Carolina]; Roman (1970) [beetles, France and Switzerland]; Scheerpeltz and Höfler (1948) [beetles, Austria]; and Weiss and West (1920, 1921a, 1921b) [insects, eastern United States].

Information on the feeding habits of particular families or genera are usually included within taxonomic papers and are not readily available to the general biologist or ecologist. Host preference in the Ciidae has been discussed by Paviour-Smith (1960a) [England], Ackerman and Shenefelt (in press) [Wisconsin], and Lawrence (1967a, 1967b, 1971, in press) [United States]. Papers on the inhabitants of a single host species include those of D. Pielou and his group (Pielou, 1966; Matthewman and Pielou, 1971; Pielou and Matthewman, 1966; Pielou and Verma, 1968) on *Fomes fomentarius* and *Piptoporus betulinus* in eastern Canada; Borden and McClaren (1970 and in press) on *Cryptoporus volvatus* in western Canada; and Paviour-Smith (1960b) on *P. betulinus* in England. Among the numerous examples of individual life history studies are those of Paviour-Smith (1963, 1964, 1965a, 1965b) on *Tetratoma fungorum* (Fabricius) and those of Heatwole and Heatwole (1968), Liles (1956), and Pace (1967) on *Bolitotherus cornutus* (Panzer).

The main purposes of the present paper are 1) to discuss the classification of the Polyporaceae and related Basidiomycetes in order to establish a sound basis for studies of host preference in Ciidae and other fungus-feeding arthropods; 2) to examine possible structural and chemical characteristics of the fruiting bodies which may serve as clues in host selection or at least account for the discriminate use of host species; and, 3) to present host records gathered to date for North American ciids and to explore methods of analyzing this data which may be of use in future ecological studies.

Methods

The host records cited in this paper are based on the following types of data: 1) Samples of Ciidae extracted in the field or laboratory from fungus fruiting bodies collected by me personally. 2) Samples extracted in the laboratory from fruiting bodies collected by colleagues in the field. 3) Samples extracted from dried fruiting bodies in a herbarium (mainly the U.S.D.A. herbaria at Beltsville, Maryland). 4) Collections made by R. C. Graves and H. S. Dybas from both field and herbarium specimens. 5) Insect specimens bearing pieces of dried fruiting body on the pin. 6) Insect specimens with host data on the label. 7) Host records from the literature.

Samples extracted by me were either pinned or placed in fluid (usually 80% ethanol) and stored in my personal collection or that of the M.C.Z. All specimens from a single collection (one fruiting body or several growing together) were given the same lot number. Specimens of the host fungus were either sent out to specialists or identified by me. Voucher specimens were retained in most instances, but with certain common fungi this was not done. Collections made by Graves were identified by L. R. Hesler, while those of Dybas were determined by J. A. Stevenson, with voucher specimens placed in the Field Museum.

Host records in categories 1 through 5 are considered to be the most reliable, since the ciids were examined by me and the fungus identifications are relatively certain or at least capable of verification. These verified or verifiable records are the only ones used in the analysis of the host data. The records in categories 6 and 7 may be mentioned in the text, but are referred to as unverified (UV).

Verified records are further divided into those which definitely represent a breeding population and those which may be accidental. A breeding record consists of any one of the following: 1) Ten or more fully pigmented adults. 2) Two or more teneral adults. 3) One teneral and two or more fully pigmented adults. 4) One or more larvae and/or pupae (when these can be identified). This breakdown is somewhat arbitrary, but it tends to eliminate accidental records, which are common enough, especially in situations where several very different host fungi (such as *Phellinus gilvus*, *Bjerkandera adusta*, *Hirschioporus pargamenus*, and *Coriolus versicolor*) grow on a single log. Cross-contamination in shipment may also account for a certain percentage of accidental occurrences. The added weight given to the presence of teneral individuals is based on the assumption that dispersal flights occur only after full pigmentation (and thus hardening of the cuticle) has been attained. Thus, a teneral adult (if it does not represent a contaminant from an adjacent fruiting body) has almost certainly developed *in situ*.

In the main data section (pp. 190–207), for each ciid species known from fungi, a brief statement of geographic distribution is given, and this is followed by a summary of host data containing the following information: 1) number of fungus species from which the ciid has been recorded; 2) number of breeding hosts (in parentheses); 3) total number of host records; 4) number of breeding records (in parentheses); 5) "niche breadth" for those species with five or more breeding records (*see* p. 181); 6) host preference group (*see* pp. 182–187); 7) number of records (nonbreeding, breeding, and total) and percentage of breeding records for each host species; and, 8) discussion, which may include host data on related extralimital species.

In Table 1, this data is further condensed and summarized. The Ciidae are arranged according to Lawrence (1971) and each is given a number that is used in the host index on page 207. A rough idea of distribution is given by indicating which adjacent geographic sectors (NW, NE, SE, SW) are included within the greater part of the range (excluding disjunct montane populations). These sectors, which are also referred to in Table 2, are based on figure 87 in Lawrence (1971). The SW sector includes southern California, Arizona, New Mexico, Texas (west of the Pecos River), and western Mexico, while the NE sector is bordered by Manitoba, the Dakotas, Nebraska, Kansas, Missouri, Kentucky, and Virginia.

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THE HOST FUNGI

North American species of Ciidae have been recorded from the fruiting bodies of 117 host fungi, nearly all of which are wood-rotting members of the advanced basidiomycete order Polyporales and are usually referred to as polypores or bracket fungi. Spores of these fungi usually germinate in dead wood, in the wounds of living trees, or in trees that have been weakened by insect attack. In some instances, access to the wood is gained through the entrance and exit holes of xylophagous insects, such as bark beetles. The mycelium of the fungus penetrates the woody tissue and causes "white rot" if cellulose and lignin are hydrolized, or "brown rot" if cellulose alone is affected. The location of the rot varies with the fungus species, and may be restricted to sapwood, heartwood, roots, or branches. Although a number of polypores are parasitic, most of those considered here are saprobes and occur primarily on dead trees and logs.

Structure and Development of the Fruiting Body

The primary mycelium, which develops from a single spore, consists of branches or hyphae that are composed of uni-nucleate cells. When anastomosis occurs with another primary mycelium, the resulting bi- or pluri-nucleate hyphae are referred to collectively as the secondary mycelium. When environmental conditions are proper, this secondary mycelium gives rise to a fruiting structure.

The fruiting body of a basidiomycete fungus is usually called a sporophore, basidiocarp, or hymenophore, and in the Polyporaceae it is often referred to as a bracket or conk. In gross structure, it usually consists of two main parts: the sterile upper portion or pileus and the reproductive layer or hymenium, which contains the spore-bearing basidia and associated cells. In most higher Basidiomycetes, the lower part of the pileus is produced to form gills, spines, or tubes, each of which is lined by hymenial surface; these structures are often called the dissepiments. The major part of the sterile tissue making up the pileus is called the context, while that forming the dissepiments is known as the trama. In some polypores, the tubes are sharply separated from the pileus, but in others the context and tramal tissue cannot be distinguished.

The form of the fruiting body varies considerably, even within a single species. In some groups it may be resupinate, that is, lying flat against the substrate with no true pileus and only the hymenial surface free. In most species, it forms a definite pileus, which may be stipitate or broadly attached to the substrate. Other modifications include a central core or a specialized upper surface, consisting of various kinds of hairs or a solid cuticle. In the majority of species, the fruiting body is annual, but in certain groups new layers of tubes are formed each year.

In most of the fungi considered here the dissepiments consist of tubes, so that the lower surface is poroid. In a few groups, however, these pores are irregular and maze-like (daedaloid), in others they break down, forming spines (irpiciform), and in certain species they are elongate so that gills are formed. In some groups, the dissepiments are lacking and the hymenial surface is flat. Although the form of the dissepiments is more constant than that of the pileus, it is notoriously variable in certain polypore species (*Daedaleopsis confragosa*) and is a poor indicator of generic or familial relationships (see below). (Bessey, 1950; Cunningham, 1965; Overholts, 1953; Snell and Dick, 1971; Teixeira, 1962).

The first undifferentiated and indefinitely growing hyphae of the secondary mycelium are called generative hyphae (Corner, 1932a,b), and they, in turn, may produce specialized branches or special microstructures, such as setae, cystidia, or basidia. Pinto-Lopes (1952) refers to all modified hyphae as tertiary hyphae, but most authors use a different terminology, discussed below. The generative hyphae are thin-walled and septate, and they usually have nodose septa or clamp connections. The loss of clamp connections (simple-septate condition) is considered important in classification, although it is thought to have occurred several times (Nobles, 1958; Teixeira, 1962).

In some species, the generative hyphae grow and branch, forming the context, surface, and dissepiments, but they never form special branches of limited growth, and normally their walls do not become thickened or discolored; Corner called this type of fruiting body monomitic, since it contains only generative hyphae. In other fungi, the generative hyphae produce a number of thick-walled and commonly aseptate specialized branches, which are of two main types: skeletal hyphae, which are broader and unbranched, growing parallel to one another, and binding hyphae, which are narrow and much-branched, forming an intricate network, and of limited growth. Fruiting bodies with skeletal or binding hyphae in addition to the generative hyphae are said to be dimitic, while those with all three types are trimitic (Corner, 1953). It is usually the skeletal hyphae that have very thick and darkly pigmented walls. Although Corner's system is an excellent descriptive tool, it has caused difficulties when applied uncritically by taxonomists (see below). The skeletal hyphae of the bovista type described by Cunningham (1947) are considered to be binding hyphae by Corner (1953), while Teixeira (1962) mentions several terms (arboriform, vermiform, etc.) used to describe individual hyphal types. One of the main difficulties in using such terms as dimitic and trimitic is that the hyphae do not remain the same in all parts of the fruiting body. In species of *Ganoderma*, for instance, the context is trimitic and the dissepiments are dimitic (Hansen, 1958), whereas in *Laetiporus sulphureus* the context is dimitic with binding hyphae and the trama monomitic (Corner, 1953).

Classification of the Host Fungi

Since this paper will serve as a basis for further studies of host preference in fungus-feeding arthropods, the classification of the polypores and their relatives will be treated in some detail. The necessity for this is partly due to the fact that American mycologists working on higher Basidiomycetes have until recently used an extremely conservative generic classification, which allows one to make very few generalizations about feeding preferences and renders useless generic determinations, such as *Fomes* sp. or *Polyporus* sp. The fact that a particular gall maker is restricted to the genus *Quercus* or that certain adult bees prefer the flowers of *Clarkia* is a useful piece of biological information. In contrast, the fact that a fungus beetle prefers species of *Fomes* is almost meaningless, since that genus in Overholts' manual (1953) contains a number of unrelated forms whose only character in common is a tendency for the fruiting body to be perennial, adding new hymenial layers each year.

The earliest generic concepts in this group date back to Fries, whose work spanned more than fifty years, beginning in 1821 and culminating with "Hymenomycetes Europaei" in 1874. Fries and his followers recognized about ten segregates based on gross structure of the fruiting body and form of the dissepiments; these include *Polyporus, Fomes, Daedalea, Poria, Trametes,* and *Hexagona,* among others. According to Donk (1971), the first real break with the Friesian system was made by Patouillard (1900), who made use of microstructural details and proposed a strongly modified classification of the Hymenomycetes. It is unfortunate that the contemporary American specialists represented two extreme schools. The conservative Lloyd ridiculed the work of Patouillard, while Murrill, a radical splitter, proposed many monotypic genera for the New World polypores. The result was that Overholts (1953) retained the old Friesian system advocated by Lloyd, and the same treatment with few modifications is found in recent manuals by Lowe (1957, 1966), and Lowe and Gilbertson (1961a,b). In Europe, on the other hand, Patouillard's system was further modified and eventually gave rise to the modern classifications of Donk (1933) and Bondarzew and Singer (1941).

The classification adopted here for the North American host fungi (see below) follows Bondarzew and Singer for the most part, but also incorporates recent changes made by Kotlaba and Pouzar (1957), Donk (1966), and others. Murrill's genera have been used for certain New World forms not treated in European manuals. Further notes on the placement of individual species are given in the next section.

Detailed reviews of the methodology used in polypore taxonomy are given by Teixeira (1962) and O. Fidalgo (1968). Excluding gross structure of the fruiting body, the following classes of characters are most frequently used: (1) generative hyphae and clamp connections, (2) modified hyphae and hyphal systems, (3) surface characters of the pileus, (4) hymenial structures, (5) spores, and (6) cultural characters.

Examples of gross habitus characters used by the early workers are resupinate condition of the sporophore (*Poria*), perennial sporophore with layers of tubes (*Fomes*), uneven tube depth (*Trametes*), gilled hymenium (*Lenzites*), and maze-like or daedaloid hymenium (*Daedalea*). Ames (1913) attempted to describe the gross consistency of the context, using such terms as coriaceous, tough-fleshy, spongy, and woody.

Clamp connections and hyphal systems have been described above. The presence of clamps is thought to be the primitive condition and occurs in the majority of genera; the simple-septate condition is found in *Oxyporus, Laetiporus, Rigidoporus, Heterobasidion,* and all of the Hymenochaetaceae. Condition of the modified hyphae has been a widely used character, especially since the publication of Corner's papers on hyphal systems (1932a,b). The "trametoid" and "fomitoid" groups discussed below are all characterized by having a trimitic hyphal system, in which both binding and skeletal hyphae are present in the context. The major difficulties in using Corner's terminology are as follows: (1) use of only three terms to describe a wide variety of hyphal types in differing combinations is too simplistic; (2) the proper analysis of the hyphal system requires careful and tedious dissection, although recent developments with ultrasounds (O. Fidalgo, 1967) have helped considerably; (3) condition of the hyphae may vary with age and position in the fruiting body; and, (4) the development of supportive structures, such as skeletal or binding hyphae, is correlated with the evolution of larger fruiting bodies and may have occurred several times independently (Donk, 1971). The most extensive use of hyphal systems was made by Cunningham (1947, 1954, 1965) in his studies of New Zealand and Australian polypores.

The color of hyphal walls, and particularly the change in color produced by potassium hydroxide, has been used frequently in polypore classification. In the Hymenochaetaceae and in many of the "fomitoids" such as *Gloeophyllum* and some *Ganoderma,* the application of KOH solution will turn the tissue permanently black. This character appears to play an important role in host preference and is discussed further on pages 174 and 176.

Teixeira (1962) discusses surface characters in detail, emphasizing the micromorphological studies made by Lohwag (1940). Spore characters were used extensively by Murrill (1907, 1908) but have not been emphasized by recent workers, at least at the generic level. Spore color may be quite variable, but the complex spore covering found in *Ganoderma* is correlated with a number of other characters of the sporophore. Hymenial structures were used by Patouillard (1900) and especially by Donk (1933) to define genera, but authorities disagree as to their importance. The presence of setae (dark, thick-walled, lance-like projections) characterize most of the Hymenochaetaceae, while certain other groups, such as *Oxyporus* and *Hirschioporus* have cystidia (blunt and thin-walled, colorless projections), which are often covered with crystals of calcium oxalate.

The most recent set of characters to be used in polypore classification are the so-called cultural characters, that is, the structure and behavior of sterile hyphae grown in culture. The most important papers on this subject are those of Nobles (1958, 1965, 1971). In addition to several hyphal features, such as the presence of clamps, other characters, such as the production of extracellular oxidase and infertility phenomena are considered.

Annotated List of Host Species

The following list includes the complete citation for every host species and the more commonly encountered synonyms of each. In the majority of cases, the species names are the same as those used in my recent revision of the North American Ciidae (Lawrence, 1971); exceptions are as follows: *Oxyporus populinus* (= *Fomes connatus*), *Dichomitus squalens* (= *Polyporus anceps*), *Lenzites elegans* (= *Daedalea ambigua* and *D. elegans*), and *Inonotus rheades* (= *Polyporus vulpinus*). The generic concepts, on the other hand, are completely different and are discussed briefly below. An attempt was made to avoid new combinations, but some of those listed could not be found in the mycological literature available to me. The order in which the genera are placed will be followed throughout the text.

HETEROBASIDIAE
AURICULARIALES
AURICULARIACEAE

Auricularia. The fruiting bodies of these fungi are soft and gelatinous, but when they dry out they become rubbery or hard and may be relatively persistent.

Auricularia auricula (Linnaeus ex Hooker) Underwood

Auricularia polytricha (Montagne) Saccardo

HOMOBASIDIAE: HYMENOMYCETES
AGARICALES

Most of the records for the Agaricales are from members of the Tricholomataceae in the sense of Singer (1951). All those encountered are lignicolous and have relatively durable fruiting bodies, in contrast to most members of the order. Occurrences on the ground-dwelling *Boletus* and *Russula* appear to be incidental nonbreeding records.

TRICHOLOMATACEAE

Lentinus crinitus Linnaeus ex Fries
Panellus stipticus (Bulliard ex Fries) Karsten
Pleurotus ostreatus (Jacquin ex Fries) Quelet
Pleurotus sp.
Schizophyllum commune Fries

BOLETACEAE

Boletus sp.

RUSSULACEAE

Russula sp.

POLYPORALES (= *APHYLLOPHORALES*)

MERULIACEAE

Phlebia merismoides Fries. The fruiting body of this species is thin and sheet-like.

THELEPHORACEAE

Species of *Stereum* are common hosts for certain ciids. Their fruiting bodies are very thin and somewhat rubbery at first, but upon drying out they become rigid. *Lopharia papyrina*, placed in a distinct genus following Boidin (1959), has a very thin and almost paper-like, violet or brownish sporophore.

Stereum hirsutum (Willdenow) Persoon ex Fries
Stereum ostrea (Blume and Nees) Fries [= *Stereum fasciatum* (Schweinitz) Fries]
Stereum sp.
Lopharia papyrina (Montagne) Boidin

HYDNACEAE

Steccherinum ochraceum Persoon ex Gray

POLYPORACEAE

This includes the majority of woody fungi serving as hosts for Ciidae, but in the present treatment *Phellinus* and its allies are excluded (see below).

Poria. This genus, as it is here constituted, contains only a few species, none of which represent major hosts. The remainder of the resupinate polypores included in *Poria* by Lowe (1966) have been placed in other genera, such as *Oxyporus, Rigidoporus*, and *Phellinus* (see below).

Poria carbonica Overholts
Poria corticola (Fries) Cooke
Poria versipora (Persoon) Romell

Polyporus. In the more conservative system of Overholts (1953) and others, this genus would include the majority of polypore species, but here it is restricted to those stipitate species related to *P. squamosus*. The fruiting body is quite soft and fleshy at first, but later it becomes harder and more durable with felt-like context tissue. According to Corner (1953), this is caused by the late development of binding hyphae and thickening of hyphal walls. The same author comments on the similarity in micromorphological detail between this species and certain *Pleurotus* (Agaricales).

Polyporus mutabilis Berkeley and Curtis
Polyporus squamosus Micheli ex Fries
Gloeoporus dichrous (Fries) Bresadola
Hapalopilus alboluteus (Ellis and Everhart) Bondarzew and Singer
Hapalopilus fibrillosus (Karsten) Bondarzew and Singer
Laetiporus sulphureus (Bulliard ex Fries) Bondarzew and Singer. This is the common sulphur bracket, which is bright yellow, soft, and fleshy, and which usually grows at the bases of dead trees, both hardwoods and conifers. Older fruiting bodies become somewhat cheesy and crumble easily. Hyphal development of this species has been described by Corner (1953).

Tyromyces. This genus includes a few minor hosts, which may not all be related. The first three have relatively soft, annual fruiting bodies, with a monomitic hyphal system. *T. spraguei* is included for convenience on the basis of Murrill's placement.

Tyromyces albellus (Peck) Bondarzew and Singer

Tyromyces cinerascens (Bresadola) Bondarzew and Singer

Tyromyces galactinus (Berkeley) Bondarzew

Tyromyces spraguei (Berkeley and Curtis) Murrill

Bjerkandera. *B. adusta* and the related *B. fumosa* have been placed in several generic groups, including *Tyromyces, Gloeoporus,* and *Leptoporus.* The fruiting body is monomitic and remains relatively soft; the context tissue is light brown or cream, while the hymenium is dark brown. *B. adusta* is a fairly common species on dead hardwoods.

Bjerkandera adusta (Willdenow ex Fries) Karsten

Oxyporus. This genus is used here in the sense of Donk (1966), in that it includes the resupinate *O. latemarginata,* as well as the perennial *O. populinus.* In both, the context tissue is light in color and relatively soft.

Oxyporus latemarginatus (Durieu and Montagne) Donk [= *Poria ambigua* Bresadola]

Oxyporus populinus (Fries) Donk [= *Polyporus connatus* Weinmann]

Ischnoderma resinosum (Schrader ex Fries) Karsten. This has a dark brown, somewhat sappy sporophore, which becomes quite hard upon drying out; it produces white rot in conifers.

Nigroporus vinosus (Berkeley) Murrill

Fomitella supina (Swartz ex Fries) Murrill. This and the preceding are subtropical species placed in monotypic genera by Murrill (1905).

Piptoporus betulinus (Bulliard ex Fries) Karsten. This is the common birch bracket, which occurs on *Betula* throughout the Holarctic region. The fruiting body is somewhat kidney-shaped and substipitate, with a whitish context, which is fairly corky when dry, and an easily detachable hymenial region. The microstructure is complex and has been described by Corner (1953). The species is thought to be related to *P. portentosus* from Australia (Cunningham, 1965).

Cryptoporus volvatus (Peck) Hubbard. This species is unique among the polypores in that the dissepiments are almost completely enclosed by a mantle extending out from the margin of the pileus. The fungus causes a white rot in gymnosperms, and the small, globular, cream-colored sporophores are often seen on standing dead conifers which have been killed by bark beetles. The species is very common in western North America but also occurs in the Northeast and in China and Japan. Some aspects of its biology are discussed by Borden and McClaren (1970 and in press).

Laricifomes, Fomitopsis, Heterobasidion, Rigidoporus. This group of genera includes most of the species formerly placed in the genus *Fomes,* but differing from *F. fomentarius* in having hyaline hyphal walls and thus a lightly pigmented context (Sections IV and V of Lowe, 1957). The fruiting structures are usually large and perennial, with a corky or woody texture. *Laricifomes* was proposed by Kotlaba and Pouzar (1957) on the basis of the trimitic hyphal system with clamp connections. *Fomitopsis pinicola* and *F. cajanderi* are dimitic with clamps and produce a brown rot, usually in gymnosperms. *F. fraxinea* and *F. fraxinophila* are only provisionally placed here. *Heterobasidion* and *Rigidoporus* differ from the above two genera in lacking clamp connections and in other microstructural details. The species tend to have sporophores that become very hard and rigid when dry. *Heterobasidion annosum* produces a white rot of gymnosperms in Europe and North America, while *Rigidoporus* includes not only the Holarctic *R. ulmarius* but a complex of tropical forms related to *R. lignosus.*

Laricifomes officinalis (Villars ex Fries) Kotlaba and Pouzar

Fomitopsis cajanderi (Karsten) Kotlaba and Pouzar [= *Fomes subroseus* Karsten]

Fomitopsis fraxinea (Bulliard ex Fries)

Fomitopsis fraxinophila (Peck)

Fomitopsis pinicola (Swartz ex Fries) Karsten [= *Fomes marginatus* (Fries) Gillet]

Heterobasidion annosum (Fries) Brefeld

Rigidoporus lignosus (Klotzsch) Imazeki

Rigidoporus nigrescens (Bresadola) Donk

Rigidoporus rigidus (Leveille)

Rigidoporus ulmarius (Sowerby ex Fries) Imazeki [= *Fomes geotropus* Cooke, of authors]

Rigidoporus vitreus (Persoon ex Fries) Donk [= ? *Poria undata* (Persoon) Bresadola]

Rigidoporus zonalis (Berkeley) Imazeki

Antrodia and *Dichomitus*. *Antrodia* is used here in the sense of Donk (1966) and includes most of the species treated as *Coriolellus* by Bondarzew and Singer (1941). Fruiting bodies are dimitic with hyaline skeletal hyphae, and are discussed in detail by Sarkar (1959). *Dichomitus* was proposed by Reid (1965) for *D. squalens*, commonly known as *Polyporus anceps* in North America (David, 1967). It differs from *Antrodia* species in the presence of dendritically branched skeletal hyphae, and in cultural characters it resembles members of the genus *Coriolus* and their relatives (Nobles, 1958). The fungus causes white pocket rot in conifers.

Antrodia sepium (Berkeley) Donk [= ? *Coriolellus albida* (Fries) Bondarzew]

Antrodia serialis (Fries) Donk

Dichomitus squalens (Karsten) Reid [= *Polyporus anceps* Peck]

Irpex tulipiferae (Schweinitz) Fries. This species is characterized by having an irpiciform or tooth-like hymenium with encrusted cystidia, no clamp connections, and a soft-leathery, whitish context.

Hirschioporus. The species comprising this group have thin, leathery sporophores resembling those of *Coriolus*, but the hyphal system is dimitic, the context is usually duplex, the dissepiments (and sometimes the context) are violet or brownish in color, and the hymenium bears a number of crystal-encrusted cystidia. Kotlaba and Pouzar (1957) have excluded *H. pargamenus* because the context is homogeneous, but in other respects it is similar to *H. abietinus*. Other common species not yet recorded as hosts are *H. fusco-violaceus* and *H. laricinus*.

Hirschioporus abietinus (Dickson ex Fries) Donk

Hirschioporus pargamenus (Fries) Bondarzew and Singer

Hirschioporus sector (Ehrenberg ex Fries) Teng

Hirschioporus versatilis (Berkeley) Imazeki

Cerrena unicolor (Bulliard ex Fries) Murrill. This is characterized by having a violet or grayish, daedaloid pore surface, a whitish, trimitic context, and a distinct black layer beneath the surface hairs (duplex context). The species is common on hardwoods in the northeastern United States.

Trametes *and the Trametoid Genera*. The genus *Trametes* is one of the more confusing of the polypore genera and has been used in different ways by various authorities. It is sometimes treated as a form genus to include all those species in which the tubes extend to unequal depths in the context. More commonly it encompasses *Coriolus* and several related genera, such as *Pycnoporus* and *Earliella*, in which the context is whitish and homogeneous, the hyphal system trimitic with clamp connections, and the tubes unequal. O. Fidalgo (1958) has suggested that gilled and daedaloid species, such as *Lenzites betulina* and *Daedalea quercina* be included as well. In the present paper, the trametoid genera (*Trametes* to *Coriolopsis* below) are treated separately and *Coriolus*, rather than *Trametes*, is used for *C. versicolor* and its relatives. The type of *Trametes*, *T. suaveolens*, is not recorded as a host, and the three species listed under this genus are New World forms of uncertain affinities, which were placed here by Lloyd and Murrill.

Trametes cirrifer (Berkeley and Curtis) Lloyd

Trametes plebeja (Berkeley) Lloyd

Trametes robiniophila Murrill

Pycnoporus. The two species included here differ from those in *Coriolus* mainly in the bright red color of the fruiting body, which is caused, according to Cunningham (1965), by pigmented mucilage granules coating the hyphae and embedded between them.

Pycnoporus cinnabarinus (Jacquin ex Fries) Karsten

Pycnoporus sanguineus (Linnaeus ex Fries) Murrill

Coriolus. This includes the majority of poroid species belonging to the trametoid group. The context is usually whitish or cream in color and leathery in texture. *Coriolus versicolor, C. hirsutus,* and *C. pubescens* are common white rots of hardwoods in the Holarctic Region, while *C. maximus, C. pinisitus,* and *C. tenuis* are more tropical in distribution.

Coriolus biformis (Fries) Patouillard

Coriolus conchifer (Schweinitz) Patouillard

Coriolus hirsutus (Wulfen ex Fries) Quelet

Coriolus maximus (Montagne) Murrill

Coriolus pinisitus (Fries) Patouillard

Coriolus pubescens (Schumacher ex Fries) Quelet

Coriolus subectypus Murrill

Coriolus tenuis (Saccardo)

Coriolus versicolor (Linnaeus ex Fries) Quelet

Lenzites. This genus is used here for those trametoid forms in which the hymenium lines gills or daedaloid pores; in most other respects they are similar to species of *Coriolus*. In older systems, *Lenzites* was used for all gilled polypores (see *Gloeophyllum* below), while *Daedalea* was used for those with a daedaloid hymenium (see *Daedaleopsis* below). The type of the genus *Daedalea, D. quercina,* although common in North America and Europe, has never been recorded as a host for Ciidae.

Lenzites betulina (Linnaeus ex Fries) Fries

Lenzites elegans (Sprengel ex Fries) Patouillard [= *Daedalea ambigua* Berkeley]

Earliella corrugata (Persoon) Murrill [= ?*Trametes scabrosa* Persoon ex Fries]. This species is common throughout the tropics and is known under various names (Fidalgo and Fidalgo, 1966); the pore surface varies from poroid to daedaloid and the upper surface is usually encrusted and reddish at the base.

Funalia. The two species below were placed in a distinct group by Bondarzew and Singer (1941), and David (1967) has pointed out certain mycelial characters that distinguish them from related trametoids. *F. hispida* is particularly common on *Populus* and *Salix* in the more arid parts of the United States.

Funalia hispida (Baglietto) [= ?*Trametes gallica* Fries]; [= ?*Funalia extenuata* (Durieu and Montagne) Domansky]

Funalia trogii (Berkeley) Bondarzew and Singer

Coriolopsis. Included here are three primarily tropical species which have a darker context than those above. The differences between *Coriolopsis occidentalis* and *Coriolus hirsutus* are slight and the two are easily confused.

Coriolopsis crocata (Fries) Murrill

Coriolopsis fulvocinerea Murrill

Coriolopsis occidentalis (Klotzsch) Murrill

The Fomitoid Genera. The next six groups include the darkly pigmented counterparts of the trametoids, in which the hyphal system is trimitic with clamp connections, but the hyphal walls are distinctly colored (with some exceptions in the genus *Ganoderma*) and usually turn black when treated with KOH.

Gloeophyllum. The two species listed under this genus have a gilled hymenium and dark brown or reddish brown context. *Gloeophyllum saepiarium* is very common on coniferous slash in northern areas, while *G. striatum* is a tropical species usually associated with *Taxodium* and *Juniperus*: both fungi cause brown rots.

Gloeophyllum saepiarium (Wulfen ex Fries) Karsten

Gloeophyllum striatum (Swartz ex Fries) Murrill

Datronia mollis (Sommerfeldt) Donk. The name *Datronia* was proposed by Donk (1966) to replace *Antrodia,* which had been misapplied to the old *Trametes mollis. D. mollis* has a resupinate sporophore with a brownish context and large, shallow tubes. According to Cunningham (1965), the species is allied to *Osmoporus odoratus,* a species not encountered in this study.

Daedaleopsis confragosa (Bolton ex Fries) Schroeter. The fruiting body of this species is pileate and firm, with a dark brown context and a hymenium that may be poroid, gilled, or daedaloid. The sporophore of *Daedalea quercina* is usually larger, with a lighter context and very thick tube walls.

Pogonomyces hydnoides (Swartz ex Fries) Murrill. This subtropical species is characterized by having small pores, dark brown context, and coarsely hirsute upper surface. According to M. Fidalgo (1968), the species should be placed in the genus *Hexagona,* which is normally restricted to those tropical forms with large, hexagonal pores.

Fomes. As mentioned above, this name has been used for a variety of fungi with large, perennial sporophores. The type, *F. fomentarius,* and its tropical counterpart *F. sclerodermeus,* may be distinguished from other perennial species by the yellowish brown context, hard surface cuticle, trimitic hyphal system with clamp connections, and simple spores.

Fomes fomentarius (Linnaeus ex Fries) Kickx

Fomes sclerodermeus (Leveille) Cooke [= *Fomes marmoratus* (Berkeley and Curtis) Cooke]

Ganoderma. This genus contains a large number of species in which the spores have a spiny inner coat and a smooth, colorless outer coat. The species also share a number of micromorphological characters discussed in detail by Hansen (1958). As in the genus *Fomes,* the hyphal system (of the context) is trimitic, but the color of the hyphal walls varies from brown in *G. applanatum* or *G. zonatum* to yellowish or hyaline in *G. tsugae.* Some authors (Cunningham, 1965) include the darker forms in the genus *Elfvingia.* The general form of the fruiting body is also variable, being stipitate with a thin, varnished cuticle in *G. tsugae* and its relatives, and sessile with a thick, woody cuticle in *G. applanatum.*

Ganoderma applanatum (Persoon ex Wallroth) Patouillard [= *Ganoderma australe* (Fries) Patouillard]

Ganoderma brownii (Murrill) Gilbertson

Ganoderma curtisii (Berkeley) Murrill

Ganoderma fulvellum Bresadola

Ganoderma lobatum (Schweinitz) Atkinson

Ganoderma lucidum (Leysser ex Fries) Karsten

Ganoderma oregonense Murrill

Ganoderma tsugae Murrill

Ganoderma zonatum Murrill

Ganoderma sp.

HYMENOCHAETACEAE

This family includes those species with characteristic yellow-brown hyphae, permanently blackening in KOH, and a monomitic or dimitic hyphal system, always lacking clamp connections. Binding hyphae never occur in this group, and setae are usually present in the hymenium (secondarily lost in some). In addition to the "polypore" genera mentioned below, the family also includes *Hymenochaete,* formerly considered to be in the Thelephoraceae because of the flat hymenial surface.

Cyclomyces iodinus (Montagne) Patouillard. This has a small, dark brown fruiting body with a very thin layer of context tissue. The hyphal system is monomitic as in the next genus.

Inonotus. This genus, which was reviewed by Pegler (1964), contains the majority of brown, monomitic species which usually possess setae. The context may be soft and spongy when fresh, but older specimens are fibrous or woody and may be brittle. *I. corrosus* is placed here for convenience, although it was removed by Pegler. *I. munzii* is considered to be a distinct species following Gilbertson (1969).

Inonotus corrosus Murrill
Inonotus munzii (Lloyd) Gilbertson
Inonotus porrectus Murrill ?
Inonotus rheades (Persoon) Bondarzew and Singer [= *Polyporus vulpinus* Fries]
Inonotus sp.
Phaeolus schweinitzii (Fries) Patouillard. This species produces a brown rot in conifers. In microstructural details the fruiting body is similar to those of *Inonotus*.
Melanoporia nigra (Berkeley) Murrill. This is a resupinate form with deep purple coloration which soon turns black. It appears to be closely related to the perennial *Nigrofomes melanoporus* (Lowe, 1957); both species are tropical.

Phellinus. This is a large genus of perennial or persistent forms in which the hyphal system is dimitic. The texture of the context is much woodier than that in *Inonotus*, and the color is yellowish brown to reddish brown. *Phellinus gilvus* and its tropical counterpart *P. licnoides* are the commonest annual species, and both cause white rot in a variety of hardwoods. Of the perennial forms, *P. igniarius* is common on hardwoods in northern areas, *P. pini* produces a white rot in northern conifers, and *P. robiniae* is a parasite of locust trees in the eastern United States. In tropical areas, there are many closely related species.

Phellinus everhartii (Ellis and Galloway) Ames [= *Fomes praerimosus* (Murrill) Saccardo and D. Saccardo]
Phellinus ferruginosus (Schrader ex Fries) Bourdot and Galzin
Phellinus gilvus (Schweinitz) Patouillard
Phellinus igniarius (Linnaeus ex Fries) Quelet
Phellinus johnsonianus (Murrill)
Phellinus laevigatus (Fries) Bourdot and Galzin
Phellinus licnoides (Montagne) Patouillard
Phellinus pini (Broteri ex Fries) Ames
Phellinus pomaceus (Persoon) Maire
Phellinus ribis (Schumacher ex Fries) Bondarzew and Singer
Phellinus robiniae (Murrill) Ames [= *Fomes rimosus* (Berkeley) Cooke, of authors]
Phellinus robustus (Karsten) Bourdot and Galzin
Phellinus sp.

Other Fungus Species Mentioned in Text

Bjerkandera fumosa (Persoon ex Fries) Karsten
Coriolus velutinus (Fries) Quelet
Daedalea quercina Linnaeus ex Fries
Exidia glandulosa Fries [TREMELLACEAE]
"Fomes" pini-halepensis Patouillard
Hirschioporus fusco-violaceus (Ehrenberg) Donk
Hirschioporus laricinus (Karsten) Teramoto
Inonotus dryadeus (Persoon ex Fries) Murrill
Inonotus hispidus (Bulliard ex Fries) Karsten
Nigrofomes melanoporus (Montagne) Murrill
Osmoporus odoratus (Wulfen ex Fries) Singer
Piptoporus portentosus (Berkeley) Cunningham
Pseudotrametes gibbosa (Persoon) Bondarzew and Singer
Stereum rugosum Persoon
Trametes suaveolens (Linnaeus ex Fries) Fries
Tyromyces stipticus (Persoon ex Fries) Kotlaba and Pouzar

Nature of the Fungus Substrate

Since the fruiting body serves as habitat and food source for ciids and other mycetophagous arthropods, it might be well to examine a) those characteristics of the sporophore which are common to all or most of the host species and may be used in defining the general habitat, and b) those features that differ from group to group and may be involved in host selection by the beetles.

The following are some general features of the fruiting body which are shared by all or most of the fungi: 1) They grow on wood and may incorporate into their structures chemical substances derived from the wood (*see* below). 2) They are usually durable, often woody or corky, and persist long enough to be inhabited by relatively stationary insects (most boring larvae) with a life cycle exceeding several weeks. 3) They usually grow off the ground and are less likely to be subjected to rapid bacterial and fungal decay or water-logging; thus they tend to retain their chemical and structural characteristics longer than mushrooms and other ground fungi. 4) They contain a high percentage of plant chitin, which in most fungi assumes the role of cellulose in providing a skeletal framework for the cell wall. This is a linear molecule constituted entirely of β-1,4 linked N-acetylglucosamine residues (Aronson, 1965). 5) The hard texture of many sporophores may necessitate special boring adaptations in the insect inhabitants. 6) The fauna inhabiting these fruiting bodies is very diverse and contains more Coleoptera and fewer Diptera than that found in mushrooms and boletes. 7) The habitat is a very localized one, since each fungus species has a limited range of host plants, and the production of a fruiting structure is often seasonal and may involve a particular set of environmental prerequisites.

The second class of characteristics—those which differ from group to group and may be used by oligophagous insects in selecting preferred hosts—are either chemical or structural. The most obvious chemical character of the fruiting body is its color. The various pigments that produce the yellow-brown color of many hymenochaetaceous conks or the violet dissepiments in *Hirschioporus* may also produce the odors used by insects in differentiating among host species. A related feature is the color change produced by KOH. In many of the darker fruiting bodies the tissue will turn permanently black with the application of potassium hydroxide solution. The same reaction may be seen in the feces of Ciidae which have fed on sporophores of *Phellinus, Ganoderma,* and other dark forms; the fecal pellets are always black, whereas they are usually only slightly darker than the color of the context. Another less obvious feature is the presence of crystals on the cystidia or among the context hyphae; according to Overholts (1953) these are composed of calcium oxalate.

Unfortunately, there has been very little published on the biochemistry of fruiting bodies encountered in this study. Arpin and Fiasson (1971) discuss a number of fungus pigments, but few of these occur in polypores. One of the more well known is cinnabarin, which causes the bright red color in *Pycnoporus cinnabarinus.* An interesting pigment and one more relevant to the present study is hispidin, which is discussed by Bu'Lock (1967). This phenolic compound, which has been isolated from the sporophores of *Inonotus hispidus* and *Phaeolus schweinitzii,* contributes to the dark color of the conk but is also involved in the hardening of the fruiting body with age. In the unripe fruits of *I. hispidus,* there is an excess of alcohol-soluble phenolic material (from which hispidin can be extracted) and a powerful phenol oxidase system which causes polymerization of the hispidin. The resulting hispidin polymer contributes to the hardening of the tissue in the ripe conk. Hispidin is synthesized in part from breakdown products of lignin in the woody substrate; in a "white rot" fungus, such as *I. hispidus,* there is an excess of hispidin produced, which is then polymerized, but in a "brown rot" fungus, such as *P. schweinitzii,* polymerization is limited, since a lack of lignin breakdown products prevents the build up of excess hispidin. It is possible that this same system is operating in other "white rot" fungi with brownish sporophores, such as the species of *Phellinus.*

The structural features that are most likely to be involved in host preference are the thickness of hyphal walls and the branching and intertwining of context hyphae, since these are largely responsible for the consistency of the tissue on which the ciids must feed. The complexity of the hyphae may be expressed to some extent by using Corner's terms, but the limitations of this system have been discussed above (p. 168). Fruiting bodies with a monomitic hyphal system, such as those of *Bjerkandera adusta,* are usually fairly soft, since they are composed entirely of thin-walled generative hyphae; in species of *Inonotus,* however, the hyphal walls thicken with age, producing a fibrous or woody context. Dimitic species fall into two major groups, depending upon whether skeletal or binding hyphae are present. In species of *Phellinus, Rigidoporus,* and *Heterobasidion,* the context consists primarily of parallel, thick-walled, skeletal hyphae, and the result is a very hard and woody substrate. In certain other dimitic forms, such as *Polyporus squamosus* and *Piptoporus betulinus,* the major supportive structures are branched and intertwining binding hyphae, so that the tissue is more felt-like, resembling that of the next group. In trimitic species, including all of the "trametoids" and "fomitoids" discussed above, both skeletal and binding hyphae are present and the tissue is somewhat felty, leathery, or corky, but never hard and rigid.

BIOLOGY OF THE CIIDAE

Nearly all members of the family Ciidae feed in both larval and adult stages on fungal hyphae comprising the mycelia and especially the fruiting bodies of various wood-rotting Basidiomycetes. Several species have been recorded from under bark, in dead wood, in decaying branches and vines, or in the galleries of bark beetles (Donisthorpe, 1938; Reitter, 1878; Swezey, 1954), but it is likely that they were associated with fungi in these habitats.

Life Cycle

Little is known about the dispersal activities of ciids, but in spring they begin to congregate on newly formed fruiting bodies. Graves (1960) notes that individuals of *Cis levettei* often fly during daylight hours, and I have collected a female of *Cis fuscipes* flying at dusk in April. Linsley and Usinger (1944) reported on large dispersal flights of subcortical and wood-boring Hemiptera and Coleoptera encountered on spring afternoons in the Sierra Nevada; no ciids were taken in these flights, although several species are common in the area. Ciidae may fly at night, but they are almost never taken at lights.

The method of entry into the sporophore will vary with the species of beetle and the form, position, and physical condition of the fruiting body. In several California species, adults enter the sporophore from the upper surface near the base. Entry at this point will put the beetle into immediate contact with the largest mass of context tissue, which is usually the preferred food of the larvae. Occasionally individuals will enter the conk by moving through cracks in the bark and boring into the base; there may be no visible signs of entry, and yet a large colony of ciids may be present within. According to Matthewman and Pielou (1971), *Cis levettei* and *Dolichocis manitoba* will usually begin work in the upper part of the context (of *Fomes fomentarius*) and will spread through the context and "mycelial core." As the populations grow, however, the hymenium is also attacked. I have observed a similar pattern in various Ciidae attacking the larger conks of *Fomes, Fomitopsis,* and *Ganoderma,* but in thinner fruiting bodies, such as those of *Coriolus* or *Hirschioporus,* the beetles may bore into the tramal tissue just beneath the hymenium or even through the walls of the pores.

The female of *Cis vitulus* bores immediately into the fungus tissue and is usually out of sight in a short time, while the male is more active on the surface of the conk. According to Entwistle (1955), the male of *Cis bilamellatus* Wood wanders about the surface and does not take part in construction of an egg gallery. Males were observed to become excited when encountering the abdomen of a female protruding from a gallery, and this was postulated to be the stimulus for copulation, which lasted from five to ten minutes.

Oviposition behavior has been described by Chapman (1869) and Entwistle (1955). Chapman observed that the female of *Octotemnus glabriculus* (Gyllenhal) constructs a definite egg gallery with egg cavities placed irregularly along the walls. One egg is placed in each cavity, which is then closed with a tightly packed plug of frass (chewed but undigested fungus tissue). Entwistle observed similar behavior in *O. glabriculus, Sulcacis affinis* (Gyllenhal), and *Cis boleti* (Scopoli), but she noted that in *Cis bilamellatus* eggs were laid in pairs within each cavity. Graves (1960) recorded the oviposition by *Cis levettei* directly on the pore surface (probably of *Ganoderma applanatum*); the egg hatched after two days and the larva crawled into one of the tubes. I have observed the frass-plugged egg cavities of *Ceracis minutissimus* lining a gallery at the base of the hymenium of *Cerrena unicolor,* and similar cavities were constructed by *Malacocis brevicollis* in the hard context tissue of *Phellinus gilvus.* The egg-laying period appears to be several months long and there is considerable overlap in generations.

The ciid larvae, upon hatching, bore directly into the fungus tissue, and not through the frass plug. There are five larval instars in *Cis vitulus* and each stadium lasts about six or seven days. *Sulcacis curtulus* was reared through its cycle on a mash of *Coriolus versicolor* in less than 60 days, but the exact length of a generation was not determined. Entwistle (1955) found the life cycle to be about eight weeks long in *Cis bilamellatus.* She also noted that adults do not become fully pigmented for three or four weeks. According to Klopfenstein (1972), there are only three larval instars in *Hadraule blaisdelli* reared on various hosts in the laboratory; each stadium is 13 or 14 days long and the pupal stage lasts ten days, so that the total life cycle (egg to adult) is still about eight weeks in duration. Adults remain in their pupal chambers for a few days after eclosion and then bore out onto the surface of the conk. It is not known whether adults disperse immediately to other fruiting bodies or remain within the same one. It is possible that dispersal flights are stimulated by depletion of the medium or by an unfavorable change owing to fouling, dessication, or decay. Under laboratory conditions some ciids may be reared through several generations on the same piece of fungus, a record of thirteen years without added food or moisture being reported by Klopfenstein (1972) for *H. blaisdelli.*

Ecological Role, Competitors, Predators, Parasites

As mentioned above, the Ciidae are normally restricted to wood-rotting fungi and are most common in those with durable, leathery or woody sporophores. In addition, both larvae and adults feed internally within the sterile pileus, where they chew the fungal hyphae comprising the context tissue. Some species may feed on the dissepiments, but this is usually after much of the context has been exhausted (Matthewman and Pielou, 1971). Moreover, Ciidae usually concentrate on those fruiting bodies which have shed their spores and are beginning to decompose (stages III and IV of Graves, 1960) and are less common on very old conks (stage V). In perennial fruiting bodies, it is usually the upper, older portions that are attacked. In the terminology of Scheerpeltz and Höfler (1948), ciids are mycetobionts; that is, they spend most of their lives within the fungus sporophores and are entirely dependent upon them for food and shelter.

Ciidae may be contrasted with the facultative fungus-feeders or mycetophiles and with those mycetobionts which differ in their feeding habits and are thus not in direct competition with ciids. For example, certain flies and tetratomid beetles (*Tetratoma*) attack only living sporophores

(Paviour-Smith, 1960b, 1965a, 1965b); nitidulids such as *Aphenolia monogama* (Crotch) and ptiliid beetles in the Nanosellinae feed exclusively on spores (Dybas, 1956; Gillogly, 1965; Gillogly and Gillogly, 1954); aradid bugs suck the juices from fresh fruiting bodies (Korinek, 1935); many beetles in the Lathridiidae and Corylophidae are attracted to molds and other secondary fungi (Crowson, 1955); and insects such as the Psocoptera occur in very old conks where they feed on dead insect remains as well as fungus tissue (Graves, 1960).

The most important direct competitors of ciids are tenebrionid beetles presently included in the tribes Bolitophagini, Rhipidandrini, and Diaperini. In North America, the most common of these are *Bolitotherus cornutus* (Panzer), *Eleates* spp., *Diaperis maculata* Olivier, *Neomida bicornis* (Fabricius), and several species of *Platydema*. Further south and in the New World tropics, species of *Rhipidandrus, Neomida,* and *Platydema* are abundant in fungi.

Other important groups of competitors among the Coleoptera are the dorcatomine Anobiidae (*Dorcatoma, Priotoma*), bostrichids of the genus *Hendecatomus*, members of the family Peltidae (*Ostoma, Thymalus*), eustrophine Melandryidae (*Orchesia, Eustrophinus*), and the anthribid beetle *Euparius marmoreus* (Olivier) (Lawrence, unpublished data; Matthewman and Pielou, 1971; Weiss and West, 1920, 1921).

Among the Lepidoptera, tineid moths, especially the genus *Nemapogon*, are particularly common (Lawrence and Powell, 1969). In the Diptera, phorid flies of the genus *Megaselia* are generally common in this habitat, and the platypezid *Polyporivora polypori* (Willard) is a regular inhabitant of *Coriolus versicolor* (Borgmeier, 1966; Kessel, 1969). Finally, the Acarina include a number of fungus-feeding forms, particularly among the Cryptostigmata (*Carabodes*) (Matthewman and Pielou, 1971).

Predators of Ciidae include a variety of forms, many of which also work adjacent habitats, such as bark, wood, and foliage. Among these are Carabidae (*Tachys*), numerous Staphylinidae, Trogositidae (*Temnochila*), Cleridae (*Ababa, Zenodosus*), Cerylonidae, anthocorid bugs (*Lyctocoris, Xylocoris*), cecidomyid flies (*Lestodiplosis*), spiders, and mites. Parasitic Hymenoptera are probably more important in the regulation of ciid populations, and many of these appear to be restricted to fungi, if not to the ciid hosts. These include Braconidae (*Meteorus, Eubadizon*), Pteromalidae (*Janssoniella*), Eulophidae (*Astichus*), and Bethylidae (*Plastanoxus chittendenii* Ashmead and *Cephalonomia perpusilla* Evans).

PATTERNS OF HOST PREFERENCE

The following analysis is based on 2075 host records (995 breeding) presented in the next section (pp. 190–207) and summarized in Table 1. Although 74 North American Ciidae have been recorded from fungi, seven of these are known from a single occurrence, and only 51 have been collected five or more times. Five species have never been recorded as breeding in a particular host, while 11 are represented by a single breeding record and 45 are known from five or more. To some extent these figures reflect a geographic collecting bias, since many of the lower numbers represent poorly known Neotropical species extending into the southern United States. In analyzing the host data, an attempt will first be made to express the degree of host or habitat preference without reference to specific host species, and this will be followed by a discussion of particular groups of host fungi, their major features, and characteristic faunas.

Host Range and "Niche Breadth"

The host range (or the total number of fungus species with which an animal is known to be associated) gives the roughest measure of the degree of host preference, and this may be further refined by eliminating incidental or nonbreeding hosts. The North American ciid with the broadest

Table 1. Summary of host data for North American Ciidae

				Niche Breadth**		Preference Group or Preferred Host
Beetle Species	Geographical* Distribution	Fungi TOT(BR)	Records TOT(BR)	B_s	B_g	
1. Cis acritus	SW	1(1)	7(1)			Hirschioporus
2. Cis americanus	NW–SE	24(18)	69(35)	14.40		Ganoderma
3. Cis angustus	NW	3(1)	4(2)			Ganoderma
4. Cis biarmatus	NW	1(1)	10(6)	1.00		Ganoderma
5. Cis castlei	NE–SE	13(4)	27(7)	3.16		Ganoderma
6. Cis cayensis	SE	5(3)	16(7)	2.57		Phellinus
7. Cis congestus	SE	2(1)	4(2)			Coriolus
8. Cis cornelli	SE	1(1)	4(2)			Hirschioporus
9. Cis cornutus	NE–SE	2(2)	5(4)			Coriolus
10. Cis creberrimus	NE–SW	24(13)	47(18)	11.24		Ganoderma
11. Cis crinitus	SE	5(4)	10(5)	3.80		Ganoderma?
12. Cis discolor	SW	2(2)	4(2)			Ganoderma
13. Cis duplex	SW	4(4)	11(10)	3.39		Ganoderma?
14. Cis ephippiatus	NW–NE	8(3)	24(14)	2.57		Ganoderma
15. Cis floridae	SE	3(2)	5(2)			Phellinus
16. Cis fuscipes	NW–SE	13(8)	135(69)	2.82	1.48	Coriolus
17. Cis hirsutus	SE	17(9)	41(16)	7.95	4.68	Ganoderma
18. Cis horridulus	NW–NE	2(2)	22(10)	1.95	1.00	Hirschioporus
19. Cis hystriculus	NW	3(1)	29(16)	1.00		Hirschioporus
20. Cis laminatus	NE	1(0)	1(0)			
21. Cis levettei	NW–SE	19(10)	140(76)	4.79	3.55	Ganoderma
22. Cis maritimus	NW	2(2)	3(2)			Phellinus
23. Cis megastictus	NW	3(1)	3(1)			Ganoderma?
24. Cis miles	NE–SE	5(3)	13(4)			Coriolus
25. Cis niedhauki	SE	1(1)	4(2)			Phellinus
26. Cis pistoria	NW–NE	4(4)	11(8)	3.39	1.45	Coriolus
27. Cis robiniophilus	NE–SE	1(1)	3(2)			Tr. robiniophila
28. Cis rotundulus	SE	5(1)	7(1)			Ganoderma?
29. Cis stereophilus	NE–SE	2(2)	12(7)	1.82	1.00	Stereum spp.
30. Cis striolatus	NW–NE	4(4)	12(7)	3.55	2.24	Hirschioporus
31. Cis subfuscus	SE	3(2)	4(2)			Coriolus
32. Cis subtilis	NE–SE	7(3)	50(17)	2.14	1.00	Hirschioporus
33. Cis tetracentrum	SW	1(1)	6(5)	1.00		Coriolus
34. Cis tridentatus	NW	9(6)	19(12)	3.46		Ganoderma
35. Cis tristis	NE–SE	9(5)	14(7)	4.36	2.57	Coriolus
36. Cis ursulinus	SE	5(0)	5(0)			
37. Cis versicolor	NW–SW	7(4)	40(23)	2.78	2.18	Coriolus
38. Cis vitulus	NW–SW	4(3)	36(22)	1.78		Coriolus
39. Enn. aurisquamosum	NE–SE	1(0)	1(0)			
40. Enn. spenceri	NW	1(0)	1(0)			
41. Dol. indistinctus	NW–NE	3(1)	9(5)	1.95		Ganoderma
42. Dol. manitoba	NW–NE	12(7)	73(31)	2.95		Ganoderma
43. Orth. punctatus	NW–SE	1(1)	1(1)			Aur. auricula?
44. Str. bilimeki	SW	2(1)	2(1)			Coriolus?
45. Str. opacicollis	NE–SE	10(5)	48(18)	2.29	1.23	Coriolus
46. Str. opalescens	NE–SE	1(1)	3(1)			Coriolus
47. Hadr. blaisdelli	NW–SW	11(7)	19(8)	6.77		
48. Hadr. elongatula	NE	1(1)	1(1)			Ganoderma?
49. Ples. cribrum	NW–NE	3(2)	58(35)	1.51		Crypt. volvatus
50. Cer. californicus	NW–SW	20(15)	80(32)	11.20	5.89	Ganoderma?
51. Cer. curtus	SE	2(1)	4(2)			Ganoderma
52. Cer. dixiensis	SW	2(1)	12(9)	1.00		Coriolus
53. Cer. magister	SE	1(1)	4(4)			Phellinus
54. Cer. minutissimus	NE–SE	3(1)	11(9)	1.00		Cerr. unicolor

TABLE 1. (*Continued*)

Beetle Species	Geographical* Distribution	Fungi TOT(BR)	Records TOT(BR)	Niche Breadth** B_s	B_g	Preference Group or Preferred Host
55. Cer. minutus	SE	9(8)	34(24)	7.09		Coriolus?
56. Cer. monocerus	SE	1(1)	2(1)			Coriolus?
57. Cer. multipunctatus	SE	6(3)	17(13)	2.95	1.99	Ganoderma
58. Cer. nigropunctatus	SE	4(2)	14(5)	1.66		Ganoderma
59. Cer. obrieni	SW	1(1)	5(5)	1.00		Phellinus
60. Cer. pecki	NE–SE	1(1)	1(1)			Phellinus?
61. Cer. powelli	SW	2(1)	3(1)			Hirschioporus
62. Cer. pullulus	SE	10(7)	43(23)	5.13	3.09	Phellinus
63. Cer. punctulatus	NE–SE	19(9)	92(45)	4.26	2.88	Phellinus
64. Cer. quadricornis	SE	7(5)	21(13)	4.26		Coriolus?
65. Cer. sallei	NE–SE	10(6)	45(22)	2.45	1.31	Ganoderma
66. Cer. schaefferi	SE	1(0)	1(0)			
67. Cer. similis	SW	3(3)	6(6)	2.78	1.00	Ganoderma
68. Cer. singularis	NE–SE	21(9)	59(17)	6.45	2.40	Phellinus
69. Cer. thoracicornis	NE–SE	36(21)	187(73)	12.00	8.31	Hirschioporus?
70. Sulc. curtulus	NW–NE	14(7)	119(55)	3.46	2.51	Coriolus
71. Sulc. lengi	NE–SE	5(3)	20(7)	2.95		Coriolus
72. Mal. brevicollis	NE–SE	16(9)	79(37)	5.50	1.12	Phellinus
73. Rhop. americanus	NE	3(1)	3(1)			Ganoderma?
74. Oct. laevis	NW–SE	14(6)	130(63)	2.24	1.26	Coriolus

* *See* explanatory notes on p. 165.

** B_s computed for species with 5 or more breeding records. B_g computed for selected species (*see* p. 182).

host range is *Ceracis thoracicornis*, which has been recorded from 36 different hosts and is capable of breeding in at least 21 of them. Other polyphagous species are *Cis americanus* and *Cis creberrimus*, each of which is known from 24 different fungus species. As many as 26 Ciidae are recorded from more than five fungi and 15 from more than ten, but when nonbreeding hosts are excluded, these figures are reduced to 18 and four, respectively. Almost one-fourth of the species appear to be monophagous, but this is partly due to sampling error.

A more precise measure of degree of preference may be obtained by using one of the indices of ecological diversity, based on the equation $H = -\Sigma p_i \log p_i$, where p_i is the proportion of individuals of a particular species inhabiting segment i of the environment, or the proportion of individuals in a particular environment belonging to species i, depending upon whether habitat diversity or species diversity is desired (MacArthur, 1965; E. Pielou, 1969). The measure used here is a modified form of B or niche breadth, discussed by Levins (1968: 43), and defined by the equation $\log B = -\Sigma p_i \log p_i$. In the strict sense, this is a measure of the "niche" of a species in a particular community, and p_i is the proportion of individuals of that species occupying a specific habitat (or host) i. In the present treatment, B_s refers to "niche breadth" over the entire geographic range of the species, and p_i is the proportion of breeding records for a specific host. The measure B_g is similar, except that p_i is the proportion of breeding records for hosts within a certain genus of fungi. In Table 1, B_s is given for all ciids with five or more breeding records, while B_g is given for selected species only. The value of B varies from 1.00 for monophagous species to almost 15 for certain polyphagous forms.

The distribution of B_s values is shown in Figure 1, with sample size (number of breeding records) indicated by shading. The mode lies between 2.5 and 3.0, while

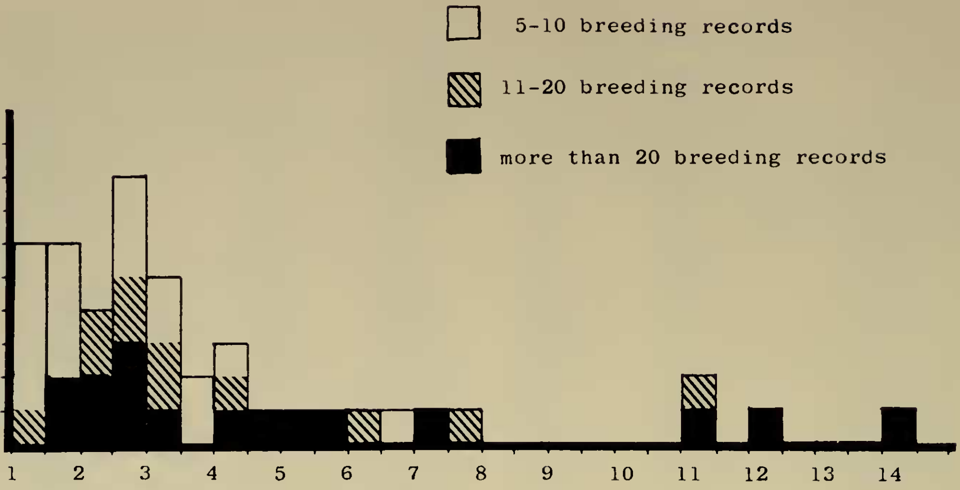

Figure 1. "Niche Breadth" Distribution and Sample Size

the median is 2.91. Although species with less than five breeding records were excluded, the B values are still correlated with sample size, and further sampling would probably eliminate several species from the first class (1.00–1.49). The majority of ciids appear to breed in several hosts, with a preference for one or two. In interpreting these values, it must be remembered that the calculations are based on all breeding records throughout the geographic range (which may be several thousand miles in diameter), and that no consideration has been given to the abundance of certain fungus species or the number of potential hosts to which a ciid has access.

The second value, B_g, based on the genera of fungi discussed on pages 169–175, gives a better idea of which species prefer a group of phylogenetically related fungi, which possess one or several sporophore characters in common and thus may be considered as one type of habitat or food source. It has been calculated for selected species, in order to illustrate how it compares with B_s in group-specific ciids and with those which are apparently less discriminate. The best example of a group-specific species with a high B_s is *Malacocis brevicollis;* although B_s is 5.5 and the number of breeding hosts is nine, almost all of the fungi are in the genus *Phellinus,* so that B_g is only 1.12. In other species, such as *Cis hirsutus,* B_g is not much lower than B_s.

Headquarters and Host Preference Groups

Paviour-Smith (1960a), in her study of host utilization by Ciidae inhabiting Wytham Woods, near Oxford, England, found that the beetles could be divided into two breeding groups and the fungi into two corresponding habitat groups, so that ciids in one group would only rarely breed in fungi of the other. She used the term "headquarters" for the one fungus species in whose fruiting bodies a particular beetle most commonly breeds and successfully completes its life cycle. Within each habitat group, a specific host might serve as headquarters for one species and be inhabited less frequently by others. These assemblages of Ciidae and their hosts are referred to here and in my earlier papers (Lawrence, 1967a, 1971, in press) as host preference groups.

The first group in the Wytham study included the common *Piptoporus betulinus* and *Ganoderma applanatum,* along with several rarer forms, such as *Polyporus squa-*

mosus, Bjerkandera adusta, Inonotus dryadeus, Phellinus pomaceus, and *Phellinus igniarius.* The Ciidae inhabiting these fungi included *Cis nitidus* (Fabricius), *Cis bidentatus* (Olivier), *Cis fagi* Waltl, *Cis bilamellatus* Wood, and *Ennearthron cornutum* (Gyllenhal). The headquarters of *Cis bilamellatus* was *P. betulinus,* while *Cis nitidus* bred most often in *G. applanatum* and *E. cornutum* preferred species of *Phellinus* (Paviour-Smith, 1969 and personal communication). *Cis bilamellatus* was usually the first species to colonize the fruiting bodies of *P. betulinus,* while *Cis bidentatus* and others were found in older conks. Paviour-Smith's second group included *Coriolus versicolor, Coriolus hirsutus, Pseudotrametes gibbosa, Lenzites betulina,* and an unidentified "*Daedalea*" among the hosts, while the Ciidae inhabiting them were *Cis boleti* (Scopoli), *Cis hispidus* (Paykull), *Strigocis bicornis* (Mellié), *Sulcacis affinis* (Gyllenhal), and *Octotemnus glabriculus* (Gyllenhal). No definite headquarters could be determined, but succession apparently took place in the conks of *C. versicolor,* with *O. glabriculus* being the first colonizer and *Cis boleti* occurring on older sporophores.

Paviour-Smith found that the main difference between fungi of the two groups, which might account for the selective utilization by ciids, was in the microstructure of the fruiting body. In the *Coriolus versicolor* group, sporophores of all species are trimitic, with both skeletal and binding hyphae, while fungi in the *Piptoporus betulinus* group are usually monomitic or dimitic. One of the more common hosts in the latter group, however, is *Ganoderma applanatum,* which is trimitic. The possibility of chemical attractants was dismissed on the grounds that old fruiting bodies are colonized after long periods of wetting and drying. The division into two host or habitat groups has been confirmed in later studies of southern European ciids (Paviour-Smith, 1969; Roman, 1970), and the same scheme, with some modifications, may be applied to the North American species as well.

The majority of North American Ciidae for which breeding hosts have been identified tends to fall into four host preference groups, as shown in Table 2. Beetles in each group are listed according to their occurrence in a particular geographic sector, as defined on page 165, and an asterisk is placed after those species common in that sector. Species that are questionably included within a group may be represented by too few breeding records or may have a broad host range including fungi in more than one group. Species placed in parentheses are common in fungi of a particular group, but still show a preference for those of another group. *Ceracis californicus,* for example, in the Northwest and Southwest sectors, appears to prefer the fruiting bodies of *Ganoderma* and yet is a fairly common member of the *Coriolus* fauna in those areas. The major characteristics of the four groups are given below, followed by a discussion of those Ciidae and host fungi which are not readily placed in any group.

The *Coriolus* Group. This is a large and well-defined assemblage corresponding to the "*Polystictus versicolor* group" of Paviour-Smith and including all of the trametoid fungi with thin, lightly pigmented, leathery fruiting bodies containing both skeletal and binding hyphae (trimitic). On the Pacific Coast, there are five common ciids, three of which extend across the northern part of the continent. *Cis fuscipes* and *Octotemnus laevis* are equally common on both coasts, while *Sulcacis curtulus* is mainly western. *Cis pistoria* is primarily a northeastern species, and in the southern part of New England, it is replaced by two species with Neotropical affinities, *Strigocis opacicollis* and *Sulcacis lengi.* In the Southeast, several other Neotropical species enter into the fauna, and *C. fuscipes* and *O. laevis* begin to drop out. The southwestern fauna includes *Cis versicolor,* which extends into Oregon, *Cis tetracentrum,* a southern mon-

Table 2. Host preference groups in North American Ciidae

Northwest	Northeast	Southeast	Southwest
CORIOLUS GROUP: Hyphae pale; hyphal system trimitic. Fruiting body thin, leathery, whitish or cream. *Pycnoporus, Coriolus, Lenzites, Earliella?, Funalia, Coriolopsis.*			
		Cis congestus	
	Cis cornutus	Cis cornutus*	
Cis fuscipes*	Cis fuscipes*	Cis fuscipes*	
	Cis miles	Cis miles*	
Cis pistoria	Cis pistoria*		
		Cis subfuscus	
			Cis tetracentrum*
	Cis tristis	Cis tristis	
Cis versicolor*			Cis versicolor*
Cis vitulus*			Cis vitulus
			?Str. bilimeki
	Str. opacicollis*	Str. opacicollis*	
	Str. opalescens	Str. opalescens	
(Cer. californicus)*			(Cer. californicus)*
			Cer. dixiensis*
		?Cer. minutus	
		?Cer. monocerus	
		?Cer. quadricornis	
	(Cer. thoracicornis)*	(Cer. thoracicornis)*	
Sulc. curtulus*	Sulc. curtulus		
	Sulc. lengi*	Sulc. lengi*	
Oct. laevis*	Oct. laevis*	Oct. laevis*	
HIRSCHIOPORUS GROUP: Hyphae pale; hyphal system dimitic. Fruiting body thin, leathery or rigid, whitish to gray or violet; hymenium violet or brown with encrusted cystidia. *Hirschioporus.*			
			Cis acritus*
		Cis cornelli	
Cis horridulus	Cis horridulus*		Cis horridulus
Cis hystriculus*			
Cis striolatus	Cis striolatus		
	Cis subtilis*	Cis subtilis*	
			Cer. powelli
	?Cer. thoracicornis*	?Cer. thoracicornis*	
PHELLINUS GROUP: Hyphae brown, black in KOH; hyphal system monomitic or dimitic. Fruiting body usually woody, perennial or persistent, sometimes fibrous, annual; usually brownish in color. *Cyclomyces, Inonotus, Phaeolus, Melanoporia, Phellinus.*			
		Cis cayensis	
		Cis floridae	
Cis maritimus			
		Cis niedhauki	
		Cer. magister	
			Cer. obrieni
	Cer. pecki	Cer. pecki	
		Cer. pullulus*	
	Cer. punculatus*	Cer. punctulatus*	
	Cer. singularis*	Cer. singularis*	
	Mal. brevicollis*	Mal. brevicollis*	

Table 2. (*Continued*)

GANODERMA GROUP: Hyphae pale to brown; hyphal system monomitic, dimitic, or usually trimitic. Fruiting body variable, usually corky to woody, perennial, and tan to brown in color. *Laetiporus, Bjerkandera, Oxyporus, Ischnoderma, Piptoporus, Laricifomes, Fomitopsis, Heterobasidion, Rigidoporus, Antrodia, Gloeophyllum, Datronia, Daedaleopsis, Pogonomyces, Fomes, Ganoderma.*

Northwest	Northeast	Southeast	Southwest
Cis americanus*	Cis americanus*	Cis americanus	
Cis angustus			
Cis biarmatus*			
	Cis castlei	Cis castlei*	
	Cis creberrimus	Cis creberrimus*	Cis creberrimus*
		?Cis crinitus	
			Cis discolor
			?Cis duplex*
Cis ephippiatus*	Cis ephippiatus		
		Cis hirsutus*	
Cis levettei	Cis levettei*	Cis levettei	
?Cis megastictus			
		?Cis rotundulus	
Cis tridentatus			
Dol. indistinctus	Dol. indistinctus		Dol. indistinctus
Dol. manitoba*	Dol. manitoba*		
	?Hadr. elongatula		
?Cer. californicus*			?Cer. californicus*
		Cer. curtus	
		Cer. multipunctatus*	
		Cer. nigropunctatus	
		(Cer. punctulatus)*	
	Cer. sallei*	Cer. sallei*	
			Cer. similis
	(Cer. thoracicornis)	(Cer. thoracicornis)	
	?Rhop. americanus		

tane form, and *Ceracis dixiensis,* which is usually associated with *Populus* at lower elevations. Two polyphagous species, *Ceracis californicus* and *Ceracis thoracicornis,* may be common inhabitants in the west and east, respectively, but each prefers a different group of fungi. It is difficult to determine any definite headquarters for most species with sufficient host records, but *Ceracis dixiensis* in the Southwest appears to be restricted to *Funalia hispida.* Like its Palaearctic counterpart, *Octotemnus laevis* prefers fresh fruiting bodies and is usually the first colonizer. Other common insects inhabiting the *Coriolus* group in eastern North America are *Neomida bicornis* (Fabricius) [Coleoptera: Tenebrionidae] and *Orchesia castanea* Melsheimer [Col.: Melandryidae].

The *Hirschioporus* Group. Although the fruiting bodies of *Hirschioporus* species resemble those of *Coriolus* and related genera, they harbor a distinct fauna in most areas studied. *Cis hystriculus* is the only common species on the west coast, while *Cis horridulus* and *Cis striolatus* are northern and montane. The main inhabitants in eastern North America are *Cis subtilis* and the eurytrophic *Ceracis thoracicornis.* Although no members of this group were found in Paviour-Smith's study area, the Palaearctic *Cis punctulatus* is known from various *Hirschioporus.*

The *Phellinus* Group. Fungi in this group are all included in the family Hymenochaetaceae and have darkly pigmented, woody or fibrous fruiting bodies without binding hyphae. The fauna is largest and most diverse in tropical regions. In the Pacific Northwest, only *Cis maritimus* is known to breed in fungi of this group, although several host species (*Phellinus gilvus, P. igniarius, P. pini, Phaeolus schweinitzii,* and certain *Inonotus*) are common in the area. The Southwest is similarly devoid of species in this group, and *Ceracis obrieni* is a Neotropical form occurring in a small area of high rainfall in southern Arizona. In both of these areas, the most common inhabitants of *Phellinus* and their relatives are moths of the genus *Nemapogon* (Lawrence and Powell, 1969). In the Northeast, *Ceracis punctulatus, Ceracis singularis,* and *Malacocis brevicollis* are all fairly common, but only the last extends into the Boreal parts of the continent. In the southeastern United States, several other Neotropical species are added to the fauna. *Malacocis brevicollis* and *Ceracis singularis* show some preference for the larger, perennial conks of *Phellinus igniarius* and *P. robiniae,* while *Ceracis punctulatus* and *Ceracis pullulus* are usually found on the smaller sporophores of *P. gilvus* and *P. licnoides.* Several ciids in this group may also occur on the more darkly pigmented fomitoids in the *Ganoderma* group. Among the Palaearctic Ciidae, *Ennearthron cornutum* (Gyllenhal) and *Cis quadridentulus* Perris occur on hymenochaetaceous hosts (Paviour-Smith, 1969; Roman, 1970). Other beetles inhabiting these fungi in eastern North America are *Platydema ellipticum* (Fabricius) [Tenebrionidae], *Orchesia gracilis* Melsheimer [Melandryidae], and *Microsternus ulkei* (Crotch) [Erotylidae] (Lawrence, unpublished data).

The *Ganoderma* Group. This is the largest and most poorly defined section, which corresponds roughly with the "*Polyporus betulinus* group" of Paviour-Smith. The fungi included form a heterogeneous assemblage with very different sporophore characteristics. *Bjerkandera adusta,* for instance, has small, pale brown fruiting bodies with a soft, monomitic context; *Fomitopsis pinicola* has large, pale, corky or woody conks with a trimitic context; and the fomitoid groups, such as *Fomes* and *Pogonomyces,* are characterized by having darkly pigmented, trimitic context tissue. In the western coniferous forests a common host is *Fomitopsis pinicola,* which may be inhabited by as many as five sympatric ciids in certain areas (although no more than three have been recorded from a single conk). In a typical situation, the fauna of *F. pinicola* will include *Dolichocis manitoba,* one member each of the *Cis americanus-tridentatus* and *Cis ephippiatus-biarmatus* species pairs (*see* p. 189), *Ostoma pippingskoeldi* (Mannerheim) [Col.: Peltidae], and a species of *Eleates* [Col.: Tenebrionidae]. In the summergreen forests of eastern North America, *Bjerkandera adusta, Fomes fomentarius, Ganoderma applanatum,* and *G. lucidum* are all abundant, and the commonest ciid species is *Cis levettei,* which coexists with *Ceracis sallei* in species of *Ganoderma.* In the northern birch forests, *Piptoporus betulinus* is also common and serves as an alternate host for *Dolichocis manitoba* and *Cis americanus,* but the more characteristic inhabitants of this fungus are *Thymalus marginicollis* Chevrolat [Col.: Peltidae], *Diaperis maculata* Olivier [Col.: Tenebrionidae], tineid moths of the genus *Nemapogon,* and various chloropid flies (Pielou and Verma, 1968). *Bjerkandera adusta* is a major host of *Cis castlei* and *Cis creberrimus* south of New England, while *Fomes sclerodermeus, Ganoderma zonatum,* and *Pogonomyces hydnoides* occur in Florida and the Gulf states, where several West Indian ciids, such as *Cis hirsutus* and *Ceracis multipunctatus* are added to the fauna. *Cis levettei* drops out in the Southeast, but *Ceracis sallei* extends into Florida, where it may coexist with *Ceracis punctulatus,* a species restricted to fungi of the *Phellinus* group in the northern parts of its range (*see* p. 189). Associated Coleoptera in the eastern United States include species of *Dorcatoma* and *Priotoma* [Anobiidae]; *Bolitotherus cornutus* (Panzer) [Tenebrionidae]; *Platydema americanum*

Laporte and Brulle [Tenebrionidae] in the Northeast; and *Neomida ferruginea* (LeConte), *Platydema ruficorne* (Sturm), and species of *Rhipidandrus* [Tenebrionidae] in the Southeast. The anthribid weevil, *Euparius marmoreus* (Olivier), is also a common inhabitant, but it has a broad host range, including fungi in other groups. In the Southwest, *Ceracis californicus* occurs on *Ganoderma* at lower elevations, while *Cis creberrimus* and *Cis duplex* inhabit *Fomitopsis* and *Ganoderma* in montane situations. Palaearctic Ciidae associated with this group include *Rhopalodontus perforatus* (Gyllenhal), *Cis bidentatus* (Olivier), and several members of the *Cis nitidus* group (Lawrence, unpublished data; Matthewman and Pielou, 1971; Paviour-Smith, 1969; Saalas, 1923).

Cryptoporus volvatus. The fauna inhabiting the sporophores of this species is a unique one, which is shared with few other fungi (*see* below). Hubbard (1892) listed 14 species from conks collected in British Columbia, Hisamatsu (1962) compared inhabitants from Japan and North America, while Borden and McClaren (1970 and in press) have treated various aspects of its biology, including arthropod infestation. The only North American ciid known to breed in *C. volvatus* is *Plesiocis cribrum*, but other common inhabitants in western North America include *Aradus debilis* Uhler [Hemiptera: Aradidae], *Morophaga cryptophori* Clarke [Lepidoptera: Tineidae]; *Megaselia polyporicola* Borgmeier [Diptera: Phoridae]; *Aphenolia monogama* (Crotch) [Coleoptera: Nitidulidae]; *Cryptophagus maximus* Blake [Col.: Cryptophagidae], *Corticaria* sp. [Col.: Lathridiidae]; and *Platydema neglectum* Triplehorn [Col.: Tenebrionidae] (Borden and McClaren, in press; Gillogly, 1965; Gillogly and Gillogly, 1954; Lawrence and Powell, 1969; Lawrence, unpublished data).

Dichomitus squalens. This species is particularly interesting because it serves as an alternate host for *Plesiocis cribrum* and certain other inhabitants of *C. volvatus*. This may be due to the fact that the two fungi often occur on the same conifer logs and are somewhat similar in the color and texture of the context. Another ciid breeding in *D. squalens* is *Cis duplex,* which also occurs on fungi in the *Ganoderma* group. According to Nobles (1971), both of these fungi resemble *Coriolus* with respect to cultural characters.

Cerrena unicolor. Fruiting bodies of this species are trametoid-like with a trimitic hyphal system and pale context, but the hymenium is grayish in color. It serves as headquarters for *Ceracis minutissimus*, which is not known to breed elsewhere, while the few other ciid inhabitants are from the *Hirschioporus* and *Ganoderma* groups. In Europe, it is a host for three ciids which also breed in *Coriolus*-group fungi.

Stereum ostrea. This fungus, which is common throughout southeastern United States, serves as headquarters for *Cis stereophilus* and the aradid bug *Mezira granulata* Say; the only other record for *C. stereophilus* is from an unidentified *Stereum.*

Auricularia auricula. This species and certain other primitive Basidiomycetes appear to harbor a distinct beetle fauna, although the data presented here are insufficient to show this. The Palaearctic literature (Benick, 1952; Falcoz, 1922) and a number of unpublished records from various parts of the world indicate that certain species of *Orthocis* and *Cis* breed in these soft and rubbery fruiting bodies and in the mycelial mats from which they arise. Further collecting in these habitats may reveal the headquarters of some of the rarer North American Ciidae.

The data presented here indicate that few, if any, Ciidae are monophagous, and probably none are totally indiscriminate in the type of fungus substrate utilized by the larvae. The great majority of species prefer a few to several hosts, most of which may be placed in one of four host preference groups, whose members share the same ciid inhabitants in any one area. These groups of host fungi and associated Ciidae are not mutually exclusive, but, with the exception of a few relatively eurytrophic species, ciids are rarely encountered breeding in hosts of the "wrong" group. These groups established on the basis of North American Ciidae are, on the whole, similar to those of Paviour-Smith for the European species, and unpublished data from the Canal Zone indicate that similar groupings occur there. Finally, there is some indication that certain other fungus inhabitants, such as tenebrionid and anobiid beetles, may show the same patterns of host preference.

Discussion

According to Dethier (1954), the problem of food plant selection may be stated in the form of two questions: "(1) how is the preference implemented? and (2) what is the genetic basis and evolutionary history of specific plant preferences?" In the following paragraphs, I will first discuss the possible mechanisms of host selection in the Ciidae and the features of various hosts which are most likely to be used in discrimination by the beetles, and then take up various evolutionary and zoogeographic factors which may have played a role in the formation of host preference patterns.

The actual mechanism by which a dispersing ciid locates a suitable fungus substrate on which to feed, mate, and/or oviposit can only be guessed at, since there have been almost no experimental studies conducted with mycetophagous insects. The initial cue may well be humidity or some other factor associated with the rotting of wood and production of fungus sporophores. The possibility that humidity is involved is supported by the fact that Ciidae have on the antennal club very large and multi-pronged basiconic sensillae (sensillifers of Lawrence, 1971), which appear to be homologous with the hygroreceptor organs of *Tribolium*, studied experimentally by Roth and Willis (1951).

At close range, a beetle may be responding to either structural (substrate consistency) or chemical stimuli, and the latter may be either gustatory or olfactory, as discussed by Thorsteinson (1960) for phytophagous insects. Since a response to taste or consistency requires physical contact, a mechanism involving either would necessitate chance colonization of individual fruiting bodies, which are often small and widely scattered. It is more likely that olfactory stimuli play a major role in locating the host, and this is supported by the fact that large numbers of ciids are commonly observed on the same conk (when they have not developed *in situ*). This leaves us with Paviour-Smith's objection that old and dead conks, which have undergone repeated wetting and drying, are still able to attract ciids, although it is unlikely that they can still produce a volatile attractant. The answer to this may lie in the work of Wood and his associates (Wood, 1932; Wood and Bushing, 1963; Wood and Vite, 1961) on host selection in bark beetles. If the first colonizing ciid reaches a fruiting body more or less by chance, and, upon receiving the proper feeding stimulus, bores into the tissue, then the beetle itself may produce a pheromone (perhaps in the feces) which would attract other members of the species in the vicinity. The initial stimulus could be variable, but the secondary mechanism would always involve olfaction. Experiments with a multiple-choice olfactometer, such as those carried out by Wood and his group, are needed to verify this.

Some of the more obvious structural and chemical features of the fruiting body which may be involved in host selection have been mentioned on pages 175–177. The leathery consistency and presence of binding hyphae characteristic of the *Coriolus* group and the woody texture and thick-walled skeletal hyphae of *Phellinus* may both represent feeding deterrents, which the beetles in each group have been able to overcome. The melanic substances found in the hyphal walls of the Hymenochaetaceae and certain "fomitoids" may be involved in the synthesis of attractants or repellents, and

Bu'Lock (1967) has shown that at least one of these (hispidin) contributes to the hardening of the tissue. Little else can be said about the chemical basis of host selection without the aid of biochemical analyses of fungal sporophores and bioassay experiments with ciids and other mycetophagous organisms.

One fact that has not been emphasized in the presentation of host data is the change in preference from one part of the geographic range to another. In general, the preferences of a species remain the same throughout the range, and most of the changes which do occur involve differences in the fungus flora. Ciidae that inhabit the fruiting bodies of *Phellinus gilvus* in the Northeast, for instance, will occupy those of its tropical counterpart *P. licnoides* in the southern part of the range. The same is true for inhabitants of *Fomes fomentarius* and *F. sclerodermeus*. Certain other floral changes occur from west to east, where gymnosperms and angiosperms, respectively, form the dominant woody substrate on which the fungi develop.

Change in host preference appears to be associated with competitive displacement in two pairs of sibling species, *Cis biarmatus-Cis ephippiatus* and *Cis tridentatus-Cis americanus*. In each case, the two species occur sympatrically along the Pacific coast, while the latter member of each pair extends across the entire northern part of the continent. In the area of sympatry, *Cis biarmatus* and *Cis tridentatus* both show a strong preference for *Fomitopsis pinicola*, while their respective siblings, *Cis ephippiatus* and *Cis americanus*, avoid this host completely, the former preferring *Ganoderma applanatum* and the latter occurring on several species, including *Bjerkandera adusta*. Where *Cis ephippiatus* and *Cis americanus* occur alone, however, both are commonly found on *F. pinicola*, as well as on other hosts. In the eastern United States, another pair of sympatric species, *Ceracis sallei* and *Ceracis punctulatus*, exhibit strong preferences for *Ganoderma applanatum* and *Phellinus gilvus*, respectively; in this case the preferences break down in Floridian populations, where the two may occur on the same fungi (*see* Lawrence, 1967b).

Certain cases of change in host preference occur in areas which are at the periphery of the geographic range and which apparently have been recently colonized. In western North America, *Dolichocis manitoba* shows a strong preference for *Fomitopsis pinicola* and occurs occasionally in other fungi of the *Ganoderma* group. The species extends across the northern part of the continent and is fairly common in New England, where it has a broader host range, including *Cerrena unicolor* and *Hirschioporus pargamenus*. One possible explanation is that the species evolved in the coniferous forests of the Northwest and has only recently invaded the Northeast, where a peripheral population is competing with a different set of species which have evolved in the eastern deciduous forest community. Similar situations occur in the Florida peninsula, which has undergone considerable change during Pleistocene flooding and is continually being colonized by wind-dispersed organisms from the West Indies. *Ceracis punctulatus*, as mentioned above, has a much broader host range in Florida than it does further north. Two West Indian species, *Cis hirsutus* and *Ceracis minutus*, occur on a variety of hosts in Florida, but both species have evolved in the Greater Antilles, where each exhibits a more definite preference for one group.

Few generalizations can be made on the possible coevolution of the Ciidae and their host fungi until more data are available on the phylogeny of the two groups. The type of close host-parasite interaction exhibited by certain plant-feeding insects probably has not occurred in the Ciidae, since the beetles are primarily saprophagous organisms, usually feeding on dead context tissue and not attacking the hymenium until after the spores are shed. Since the beetles do not interfere with the production or dissemination of spores, it is unlikely that the fungus would respond by producing toxins or repellents. This possibility should not be dismissed, however, until the biology of these organisms is more thoroughly worked out.

Several genera and species groups of Ciidae have evolved on a single type of substrate and are rarely found elsewhere. Species of *Strigocis, Sulcacis,* and *Octotemnus* are almost always associated with *Coriolus* and its relatives, as are the *boleti, fuscipes, pallidus,* and *tricornis* groups of *Cis.* Species of *Malacocis* are restricted to *Phellinus*-group fungi, as are certain sections of *Ceracis.* The Neotropical *Cis taurus* group and the Holarctic *Cis nitidus* group are usually found in fungi of the *Ganoderma* group, while exceptions in both involve a switch to the *Phellinus* group.

Although the present treatment is based primarily on data from temperate and subtropical regions, unpublished records indicate that in tropical forests the degree of host specificity may be greater than shown here. On Barro Colorado Island in the Canal Zone, the conks of *Ganoderma applanatum, Fomes sclerodermeus,* and *Pogonomyces hydnoides* have certain shared faunal elements, but in addition each is inhabited by one or more species of Ciidae and/or Tenebrionidae that are not found in the other two. An analysis of this tropical host data is now in progress.

CIIDAE AND THEIR HOST FUNGI

1. *Cis acritus* Lawrence

Geographical range. Montane regions of southern California, Arizona, and New Mexico.

Host range. Fungi: 1(1). Records: 7(1). Known from *Hirschioporus abietinus* only.

Discussion. This species is the western counterpart of *Cis subtilis.* In the mountains of the Southwest, it may be taken along with *Cis horridulus* and *Ceracis powelli* in the fruiting bodies of *Hirschioporus* on conifers.

2. *Cis americanus* Mannerheim

Geographical range. Northern part of North America, from southern Alaska to Nova Scotia, south in California to Monterey County (coastal) and Fresno County (Sierra Nevada), in the Rocky Mountain region south to northern Utah and Colorado, and in the Appalachians as far south as western North Carolina.

Host range. Fungi: 24(18). Records: 69(35). $B_s = 14.40$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Pleurotus ostreatus	2	1	3	2.8
Phlebia merismoides	1	0	1	0.0
Stereum hirsutum	2	4	6	11.4
Steccherinum ochraceum	1	2	3	5.7
Poria versipora	1	2	3	5.7
Polyporus squamosus	0	2	2	5.7
Laetiporus sulphureus	2	1	3	2.8
Bjerkandera adusta	2	6	8	17.1
Ischnoderma resinosum	0	1	1	2.8
Piptoporus betulinus	3	4	7	11.4
Fomitopsis pinicola	3	2	5	5.7
Heterobasidion annosum	3	1	4	2.8
Rigidoporus nigrescens	1	0	1	0.0
Irpex tulipiferae	1	0	1	0.0
Hirschioporus abietinus	3	0	3	0.0
Hirschioporus pargamenus	0	1	1	2.8
Coriolus biformis	1	0	1	0.0
Coriolus hirsutus	0	1	1	2.8
Coriolus versicolor	4	1	5	2.8
Datronia mollis	0	2	2	5.7
Daedaleopsis confragosa	0	1	1	2.8
Fomes fomentarius	1	0	1	0.0
Ganoderma applanatum	1	1	2	2.8
Ganoderma tsugae	2	2	4	5.7
Totals	34	35	69	100.0

Discussion. This is probably the most eurytrophic of the North American Ciidae, breeding in at least 18 different fungi belonging to various groups. As mentioned in an earlier paper (Lawrence, 1971) the species is quite variable and may represent a complex of sibling species (along with *Cis tridentatus*). There is some indication that two distinct forms with slightly different host preferences occur in California, but more field data will be necessary to determine this.

3. *Cis angustus* Hatch

Geographical range. Mountains of the

Pacific Coast from south-central British Columbia to the southern Sierra Nevada.

Host range. Fungi: 3(1). Records: 4(2). Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Laricifomes officinalis	1	0	1	0.0
Fomitopsis pinicola	0	2	2	100.0
Heterobasidion annosum	1	0	1	0.0
Totals	2	2	4	100.0

Discussion. This beetle is relatively uncommon in large and woody, pale-colored conks growing on conifers in the Northwest. It is related to the Palaearctic *Cis fagi* Waltl and *C. castaneus* Mellié, the former of which has been recorded from *Piptoporus betulinus, Laetiporus sulphureus, Inonotus dryadeus,* and *Ganoderma applanatum* (Donisthorpe, 1935; Paviour-Smith, 1960a, 1969).

4. *Cis biarmatus* Mannerheim

Geographical range. Pacific Coast of North America from southern Alaska to Marin County, California.

Host range. Fungi: 1(1). Records: 10(6). $B_s = 1.00$. Known from *Fomitopsis pinicola* only.

Discussion. *Cis biarmatus* is known only from the narrow Pacific coastal belt where it is associated with *Fomitopsis pinicola;* the closely related beetle *Cis ephippiatus* in the same area prefers the sporophores of *Ganoderma applanatum.*

5. *Cis castlei* (Dury)

Geographical range. Eastern North America, from extreme southern Ontario south to central Florida, west to Iowa, and south through eastern Mexico to Costa Rica.

Host range. Fungi: 13(4). Records: 27(7). $B_s = 3.16$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Lentinus crinitus	1	0	1	0.0
Stereum ostrea	2	0	2	0.0
Polyporus mutabilis	0	1	1	14.3
Bjerkandera adusta	5	4	9	57.1
Oxyporus latemarginata	1	0	1	0.0
Nigroporus vinosus	0	1	1	14.3
Rigidoporus lignosus	1	0	1	0.0
Rigidoporus zonalis	1	0	1	0.0
Hirschioporus pargamenus	5	0	5	0.0
Trametes plebeja	1	0	1	0.0
Earliella corrugata	0	1	1	14.3
Pogonomyces hydnoides	2	0	2	0.0
Ganoderma applanatum	1	0	1	0.0
Totals	20	7	27	100.0

Discussion. This species is known from scattered localities throughout the eastern half of the continent and is not particularly common. It is usually encountered on *Bjerkandera adusta* where it may be associated with *Cis creberrimus.*

6. *Cis cayensis* Lawrence

Geographical range. Florida Keys and Cuba.

Host range. Fungi: 5(3). Records: 16 (7). $B_s = 2.57$. Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Lopharia papyrina	1	0	1	0.0
Pogonomyces hydnoides	1	2	3	28.6
Inonotus corrosus	0	1	1	14.3
Inonotus porrectus	2	4	6	57.1
Phellinus robiniae	5	0	5	0.0
Totals	9	7	16	100.0

7. *Cis congestus* Casey

Geographical range. Southeastern United States, from Maryland south to northern Florida and west to southern Illinois and eastern Texas.

Host range. Fungi: 2(1). Records: 4 (2). Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Coriolus hirsutus	1	2	3	100.0
Coriolus pinisitus	1	0	1	0.0
Totals	2	2	4	100.0

Discussion. This is the southeastern counterpart of *Cis vitulus* and both species have an obvious preference for members of the *Coriolus* group.

8. *Cis cornelli* Lawrence

Geographical range. The Carolinas and Florida.

Host fungi. Fungi: 1(1). Records: 4 (2). Known from *Hirschioporus sector* only.

Discussion. *Cis cornelli* belongs to a large Neotropical species-group, which includes *Cis setifer* (Gorham) and *Cis taurus* (Reitter). It appears to prefer the fruiting bodies of *Hirschioporus* but its tropical relatives occur on a wide variety of other fungi. On Barro Colorado Island, Canal Zone, about ten species in this group have been collected, each preferring different host fungi.

9. *Cis cornutus* Blatchley

Geographical range. Eastern United States, from New York south to northern Florida and west to Illinois and Arkansas.

Host range. Fungi: 2(2). Records: 5 (4). Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Coriolus subectypus	0	1	1	25.0
Coriolus versicolor	1	3	4	75.0
Totals	1	4	5	100.0

10. *Cis creberrimus* Mellié

Geographical range. Eastern North America, from Vermont south to Florida and west to eastern Nebraska, Kansas, and Texas; montane regions of the Southwest; throughout the West Indies; scattered localities in Mexico, Central and South America.

Host range. Fungi: 24(13). Records: 47(18). $B_s = 11.24$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Pleurotus sp.	1	0	1	0.0
Schizophyllum commune	1	0	1	0.0
Poria corticola	0	1	1	5.6
Laetiporus sulphureus	1	0	1	0.0
Bjerkandera adusta	1	4	5	22.2
Oxyporus latemarginatus	1	1	2	5.6
Fomitella supina	1	0	1	0.0
Laricifomes officinalis	0	2	2	11.1
Fomitopsis pinicola	1	1	2	5.6
Heterobasidion annosum	0	1	1	5.6
Dichomitus squalens	1	0	1	0.0
Hirschioporus pargamenus	1	1	2	5.6
Pycnoporus sanguineus	0	1	1	5.6
Coriolus hirsutus	1	0	1	0.0
Lenzites elegans	1	0	1	0.0
Earliella corrugata	1	1	2	5.6
Funalia hispida	1	0	1	0.0
Gloeophyllum striatum	1	0	1	0.0
Pogonomyces hydnoides	2	1	3	5.6
Fomes sclerodermeus	5	1	6	5.6
Ganoderma applanatum	4	0	4	0.0
Ganoderma fulvellum	0	1	1	5.6
Ganoderma lucidum	2	2	4	11.1
Phellinus gilvus	2	0	2	0.0
Totals	29	18	47	100.0

Discussion. This is another widely distributed and eurytrophic species which breeds in at least 13 host fungi. As mentioned in an earlier paper (Lawrence, 1971) there are at least four geographical races (or perhaps species) that occur in North America. The populations are largely allopatric, and the host preferences do not differ much among the different populations. In the eastern United States, the beetle is usually encountered in small numbers under bark or in various hosts. It is usually not the dominant species in a fruiting body. Part of the reason for the wide host range may be the inclusion of several Neotropical records which may represent distinct species. The entire complex is in need of further revision.

11. *Cis crinitus* Lawrence

Geographical range. Southeastern United States, from North Carolina to Florida and west to eastern Texas; the Bahamas, and the Greater Antilles.

Host range. Fungi: 5(4). Records: 10 (5). $B_s = 3.80$. Group: *Ganoderma?*

Records.	NB	BR	TOT	%BR
Lopharia papyrina	0	2	2	40.0
Coriolopsis fulvocinerea	2	1	3	20.0
Gloeophyllum striatum	0	1	1	20.0
Pogonomyces hydnoides	2	1	3	20.0
Ganoderma zonatum	1	0	1	0.0
Totals	5	5	10	100.0

12. *Cis discolor* Lawrence

Geographical range. Montane regions of southern Arizona.

Host range. Fungi: 2(2). Records: 4 (4). Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Fomitopsis cajanderi	0	3	3	75.0
Antrodia sepium	0	1	1	25.0
Totals	0	4	4	100.0

13. *Cis duplex* Casey

Geographical range. Mountains of the southwestern United States and Mexico, from southern California east to north-central New Mexico, and south as far as Morelos and the southern tip of Baja California.

Host range. Fungi: 4(4). Records: 11 (10). $B_s = 3.39$. Group: *Ganoderma*?

Records.	NB	BR	TOT	%BR
Laricifomes officinalis	0	2	2	20.0
Fomitopsis pinicola	0	2	2	20.0
Dichomitus squalens	1	5	6	50.0
Ganoderma oregonense	0	1	1	10.0
Totals	1	10	11	100.0

Discussion. This is a relatively common species in the mountains of the Southwest where it is associated with conifers. The beetle is commonly found in the fruiting bodies of *Dichomitus squalens,* where it may coexist with *Plesiocis cribrum.*

14. *Cis ephippiatus* Mannerheim

Geographical range. Western North America, from southern Alaska south in California to Alameda County and the southern Sierra Nevada, and in the Rocky Mountain Region to northern Nevada and Colorado. Also known from Vermont, New Hampshire, and the Gaspé Peninsula of Quebec.

Host range. Fungi: 8(3). Records: 24 (14). $B_s = 2.57$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Poria versipora	1	0	1	0.0
Laetiporus sulphureus	1	0	1	0.0
Ischnoderma resinosum	1	0	1	0.0
Piptoporus betulinus	1	0	1	0.0
Fomitopsis pinicola	3	4	7	28.6
Heterobasidion annosum	1	0	1	0.0
Ganoderma applanatum	2	8	10	57.1
Ganoderma brownii	0	2	2	14.3
Totals	10	14	24	100.0

Discussion. This species occurs throughout the northern part of the continent, but most of the records are from the Pacific Coast. Where it is sympatric with the closely related *C. biarmatus,* it is usually found on *Ganoderma applanatum* or *G. brownii,* but in areas outside the range of *C. biarmatus,* it is commonly associated with *Fomitopsis pinicola.* This appears to be a case of competitive exclusion.

15. *Cis floridae* Dury

Geographical range. Southern Georgia, Florida, and Cuba.

Host range. Fungi: 3(2). Records: 5 (2). Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Lopharia papyrina	2	0	2	0.0
Phellinus gilvus	1	1	2	50.0
Phellinus sp.	0	1	1	50.0
Totals	3	2	5	100.0

16. *Cis fuscipes* Mellié

Geographical range. Widespread throughout most of northern and eastern North America, from northern British Columbia south to Los Angeles County in California, east across Canada to Nova Scotia, and south throughout eastern and midwestern United States (east of the 100th meridian) to southern Texas and Florida. Also known from Cuba, Madeira, and Hawaii.

Host range. Fungi: 13(8). Records: 135(69). $B_s = 2.82$. $B_g = 1.48$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Polyporus squamosus	0	1	1	1.4
Bjerkandera adusta	0	1	1	1.4
Fomitopsis fraxinea	1	0	1	0.0
Fomitopsis pinicola	1	0	1	0.0
Coriolus conchifer	1	2	3	2.9
Coriolus hirsutus	4	10	14	14.5
Coriolus pubescens	4	2	6	2.9
Coriolus subectypus	1	0	1	0.0
Coriolus versicolor	43	49	92	71.0
Lenzites betulina	9	3	12	4.3
Lenzites elegans	1	0	1	0.0
Ganoderma applanatum	1	0	1	0.0
Ganoderma brownii	0	1	1	1.4
Totals	66	69	135	100.0

Discussion. Cis fuscipes is the widespread and parthenogenetic beetle which has been discussed at length elsewhere (Lawrence, 1967a, 1971). Because of the large number of collections made for this species, its preference for members of the *Coriolus* group is well established. Its relatives in eastern Asia appear to have similar preferences (Chujo, 1939; Fukuda, 1940; Lawrence, 1967a).

17. *Cis hirsutus* Casey

Geographical range. Florida, the Bahamas, and the Greater Antilles.

Host range. Fungi: 17(9). Records: 41 (16). B_s = 7.95. B_g = 4.68. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Auricularia polytricha	1	0	1	0.0
Fomitella supina	1	0	1	0.0
Rigidoporus rigidus	1	0	1	0.0
Hirschioporus pargamenus	0	1	1	6.2
Hirschioporus sector	0	1	1	6.2
Coriolus maximus	2	0	2	0.0
Coriolus pinisitus	2	0	2	0.0
Lenzites elegans	1	0	1	0.0
Earliella corrugata	1	2	3	12.5
Coriolopsis fulvocinerea	1	1	2	6.2
Pogonomyces hydnoides	8	3	11	18.7
Fomes sclerodermeus	4	1	5	6.2
Ganoderma applanatum	1	0	1	0.0
Ganoderma lucidum	0	1	1	6.2
Ganoderma zonatum	1	3	4	18.7
Ganoderma sp.	0	3	3	18.7
Cyclomyces iodinus	1	0	1	0.0
Totals	25	16	41	100.0

Discussion. Although this is primarily an Antillean species, most of the host records are from southern Florida. The Floridian records indicate that the species breeds on a wide variety of fungi, but it is quite possible that the host range is narrower in more stable areas (the larger islands) closer to the center of distribution (*see* p. 189). There appears to be a preference for *Pogonomyces hydnoides* and species of *Ganoderma.*

18. *Cis horridulus* Casey

Geographical range. Northern and montane regions of North America, except Pacific Coast, ranging from south-central British Columbia to the Atlantic Coast, south in the Rocky Mountain Region as far as the Chiricahua Mountains of Arizona, and along the Appalachian Chain as far as western North Carolina.

Host range. Fungi: 2(2). Records: 22 (10). B_s = 1.95. B_g = 1.00. Group: *Hirschioporus.*

Records.	NB	BR	TOT	%BR
Hirschioporus abietinus	5	4	9	40.0
Hirschioporus pargamenus	7	6	13	60.0
Totals	12	10	22	100.0

Discussion. This species and *C. hystriculus* are part of a northern complex which includes the Palaearctic *Cis punctulatus* Gyllenhal and *C. tomentosus* Mellié. All of these forms breed in the fruiting bodies of various *Hirschioporus,* primarily in the northern coniferous forests. In eastern North America, *C. horridulus* appears to be equally common in *H. abietinus* and *H. pargamenus,* which occur on conifers and hardwoods, respectively. In the Old World, *C. punctulatus* has been recorded from *H. abietinus* and *H. fuscoviolaceus* (Benick, 1952; Lohse, 1967; Saalas, 1923; Scheerpeltz and Höfler, 1948).

19. *Cis hystriculus* Casey

Geographical range. Western British Columbia, Washington, and Oregon, south through the Sierra Nevada and coastal California to the Transverse Ranges in the southern part of the state.

Host range. Fungi: 3(1). Records: 29 (16). B_s = 1.00. Group: *Hirschioporus.*

Records.	NB	BR	TOT	%BR
Poria versipora	1	0	1	0.0
Tyromyces cinerascens	1	0	1	0.0
Hirschioporus abietinus	11	16	27	100.0
Totals	13	16	29	100.0

Discussion. This is the western counterpart of *Cis horridulus,* and it may not be a distinct species. It is the most common insect inhabiting *Hirschioporus abietinus* on the Pacific Coast.

20. *Cis laminatus* Mellié

Geographical range. In North America, known from Albany, New York. In Europe, recorded from France, Italy, Germany, Poland, Czechoslovakia, and Hungary.

Host range. In North America, known from *Cryptoporus volvatus* only. In Europe, recorded from "*Fomes*" *pini-halepensis, Pseudotrametes gibbosa,* and *Tyromyces stipticus* (Peyerimhoff, 1919; Scheerpeltz and Höfler, 1948; Roman, 1970).

Records. A single unverified record from *C. volvatus.*

Discussion. This species has not been collected since 1920 and may not be established in North America.

21. *Cis levettei* (Casey)

Geographical range. Widespread in North America east of the 100th meridian, from Newfoundland south to Alabama and west to Manitoba, Kansas, and Texas. In the western part of the continent, recorded from Alberta, northwestern Colorado, eastern British Columbia, Washington, and California.

Host range. Fungi: 19(10). Records: 140(76). $B_s = 4.79$. $B_g = 3.55$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Stereum ostrea	2	0	2	0.0
Polyporus squamosus	2	0	2	0.0
Bjerkandera adusta	1	0	1	0.0
Oxyporus populinus	1	3	4	3.9
Ischnoderma resinosum	0	1	1	1.3
Piptoporus betulinus	1	1	2	1.3
Fomitopsis pinicola	3	13	16	17.1
Rigidoporus nigrescens	0	1	1	1.3
Rigidoporus vitreus	1	0	1	0.0
Hirschioporus pargamenus	2	0	2	0.0
Coriolus pubescens	2	0	2	0.0
Coriolus versicolor	3	0	3	0.0
Lenzites betulina	1	0	1	0.0
Daedaleopsis confragosa	0	2	2	2.6
Fomes fomentarius	6	12	18	15.8
Ganoderma applanatum	32	37	69	48.7
Ganoderma lucidum	1	1	2	1.3
Ganoderma tsugae	5	5	10	6.6
Phellinus robiniae	1	0	1	0.0
Totals	64	76	140	100.0

Discussion. Cis levettei occurs throughout central and eastern North America, but it is most common in the Northeast. It is usually found breeding in *Ganoderma applanatum,* but it is also relatively common in the conks of *Fomes fomentarius, Fomitopsis pinicola,* and *Ganoderma tsugae.* According to Matthewman and Pielou (1971), this species is the second most common beetle infesting the sporophores of *F. fomentarius* in Quebec, where it is most often associated with the anobiid *Dorcatoma dresdensis* (Herbst) and the tenebrionid *Bolitotherus cornutus* (Panzer). In the fruiting bodies of *G. applanatum,* it is often found along with *Ceracis sallei. Cis levettei* belongs to a group of species which includes the Palaearctic *Cis nitidus* (Fabricius), *C. jacquemarti* Mellié, *C. glabratus* Mellié, *C. hanseni* Strand, and *C. lineatocribratus* Mellié. Most of the members of this group have similar host preferences, being most commonly encountered in *G. applanatum, F. fomentarius,* and *F. pinicola,* but it is not clear from the literature whether or not they further subdivide the habitat in areas of overlap (Benick, 1952; Paviour-Smith, 1960a, 1969; Peyerimhoff, 1915; Roman, 1970; Scheerpeltz and Höfler, 1948).

22. *Cis maritimus* (Hatch)

Geographical range. Pacific Coast from southwestern British Columbia to extreme northwestern California. Also known from south-central Manitoba.

Host range. Fungi: 2(2). Records: 3 (2). Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Phaeolus schweinitzii	1	1	2	50.0
Phellinus pini	0	1	1	50.0
Totals	1	2	3	100.0

Discussion. According to the few records available, this species appears to prefer the xanthochroic fruiting bodies of *Phaeolus* and *Phellinus,* which is unusual both for the species-group (*Cis nitidus* group) and the geographic area. Although both *Phaeolus schweinitzii* and *Phellinus pini* are common in the Pacific Northwest, *C. maritimus* is the only ciid to utilize them.

23. *Cis megastictus* Lawrence

Geographical range. Montane regions of northern California.

Host range. Fungi: 3(1). Records: 3 (1). Group: *Ganoderma?*

Records.	NB	BR	TOT	%BR
Laetiporus sulphureus	1	0	1	0.0
Fomitopsis pinicola	1	0	1	0.0
Heterobasidion annosum	0	1	1	100.0
Totals	2	1	3	100.0

24. *Cis miles* (Casey)

Geographical range. Eastern North America, from New York south to central Florida and west to Arkansas and Louisiana.

Host range. Fungi: 5(3). Records: 13 (4). Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Stereum ostrea	1	0	1	0.0
Fomitella supina	1	0	1	0.0
Coriolus subectypus	0	1	1	25.0
Coriolus versicolor	6	1	7	25.0
Lenzites betulina	1	2	3	50.0
Totals	9	4	13	100.0

Discussion. This is the only Nearctic member of a large Neotropical species-group which includes *Cis tricornis* Gorham and *C. delicatulus* (Jacquelin DuVal). Like most of its relatives, *Cis miles* breeds in the pale, coriaceous sporophores characteristic of the *Coriolus* group.

25. *Cis niedhauki* Lawrence

Geographical range. Known from Lignum Vitae Key, Florida.

Host range. Fungi: 1(1). Records: 4 (2). Known from *Phellinus robiniae* only.

26. *Cis pistoria* Casey

Geographical range. Northeastern North America from central Alberta to southern Minnesota and southern New England.

Host range. Fungi: 4(4). Records: 11 (8). $B_s = 3.39$. $B_g = 1.45$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Bjerkandera adusta	0	1	1	12.5
Coriolus hirsutus	0	1	1	12.5
Coriolus pubescens	0	2	2	25.0
Coriolus versicolor	3	4	7	50.0
Totals	3	8	11	100.0

Discussion. Cis pistoria is primarily a northeastern species, inhabiting *Coriolus versicolor* and its allies, and often found in association with *Cis fuscipes* and *Octotemnus laevis.* Its Palaearctic relatives, such as *Cis micans* (Fabricius), *C. villosulus* (Marsham), and *C. boleti* (Scopoli), have similar preferences, occurring on various *Coriolus,* as well as *Lenzites betulina* and *Pseudotrametes gibbosa* (Benick, 1952; Donisthorpe, 1935; Falcoz, 1921; Paviour-Smith, 1960a; Peyerimhoff, 1915; Roman, 1970; Scheerpeltz and Höfler, 1948).

27. *Cis robiniophilus* Lawrence

Geographical range. Maryland, Kentucky, and Ohio.

Host range. Fungi: 1(1). Records: 3 (2). Known from *Trametes robiniophila* only.

28. *Cis rotundulus* Lawrence

Geographical range. Southeastern United States, from North Carolina to Florida and west to eastern Texas.

Host range. Fungi: 5(1). Records: 7 (1). Group: *Ganoderma*?

Records.	NB	BR	TOT	%BR
Stereum ostrea	1	0	1	0.0
Ganoderma curtisii	2	0	2	0.0
Ganoderma lucidum	1	1	2	100.0
Cyclomyces iodinus	1	0	1	0.0
Phellinus gilvus	1	0	1	0.0
Totals	6	1	7	100.0

29. *Cis stereophilus* Lawrence

Geographical range. Eastern coast of the United States, from southern Massachusetts to northern Florida, and northeastern Mexico.

Host range. Fungi: 2(2). Records: 12 (7). $B_s = 1.82$. $B_g = 1.00$.

Records.	NB	BR	TOT	%BR
Stereum ostrea	5	5	10	71.4
Stereum sp.	0	2	2	28.6
Totals	5	7	12	100.0

Discussion. This is the only known North American ciid that breeds only in the fruiting bodies of the thelephoraceous *Stereum.* In western North America, *Cis* *americanus* may breed in *Stereum hirsutum*, but that is one of many hosts. In the European fauna, *Cis festivus* (Panzer) and *Orthocis alni* (Gyllenhal) have both been recorded from *Stereum rugosum* (Benick, 1952), while several undescribed Neotropical Ciidae have been found in association with various thelephores.

30. *Cis striolatus* Casey

Geographical range. Widespread across the northern part of North America, from northern Mackenzie District, Northwest Territory, to Nova Scotia, south into the Sierra Nevada and Rocky Mountains, in the Midwest as far as Kansas, and on the Atlantic Coast as far as northern Florida.

Host range. Fungi: 4(4). Records: 12 (7). $B_s = 3.55$. $B_g = 2.24$. Group: *Hirschioporus.*

Records.	NB	BR	TOT	%BR
Hirshchioporus abietinus	4	2	6	28.6
Hirschioporus pargamenus	1	3	4	42.8
Cerrena unicolor	0	1	1	14.3
Coriolus hirsutus	0	1	1	14.3
Totals	5	7	12	100.0

Discussion. This is another northern species that inhabits the fruiting bodies of *Hirschioporus*, but it is far less common than either *C. horridulus* or *C. subtilis.* Similar and probably related species in North America include *Cis versicolor* and *C. tristis,* both of which prefer fungi in the *Coriolus* group. Allied species in the Old World, *Cis comptus* Gyllenhal and *C. striatulus* Mellié, have been taken on *Hirschioporus abietinus, Cerrena unicolor,* and various *Coriolus* (Lawrence, unpublished data; Peyerimhoff, 1915; Roman, 1970; Saalas, 1923; Scheerpeltz and Höfler, 1948) but it is unclear just how specific each is.

31. *Cis subfuscus* Gorham

Geographical range. Central Texas south along the eastern coast of Mexico to Veracruz.

Host range. Fungi: 3(2). Records: 4 (2). Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Panellus stipticus	0	1	1	50.0
Coriolus hirsutus	1	1	2	50.0
Lenzites elegans	1	0	1	0.0
Totals	2	2	4	100.0

32. *Cis subtilis* Mellié

Geographical range. Eastern North America, from New Hampshire south to Florida and west to Illinois, Arkansas, and eastern Texas.

Host range. Fungi: 7(3). Records: 50 (17). $B_s = 2.14$. $B_g = 1.00$. Group: *Hirschioporus.*

Records.	NB	BR	TOT	%BR
Stereum ostrea	1	0	1	0.0
Bjerkandera adusta	1	0	1	0.0
Hirschioporus abietinus	6	1	7	5.9
Hirschioporus pargamenus	22	12	34	70.6
Hirschioporus sector	1	4	5	23.5
Ganoderma applanatum	1	0	1	0.0
Phellinus gilvus	1	0	1	0.0
Totals	33	17	50	100.0

Discussion. This species is the most common inhabitant of *Hirschioporus* throughout the eastern United States. It is usually found in association with *Ceracis thoracicornis,* but the latter has a much broader host range.

33. *Cis tetracentrum* Gorham

Geographical range. Mountains of southern California and Arizona, south through the Mexican highlands as far as central Veracruz.

Host range. Fungi: 1(1). Records: 6 (5). $B_s = 1.00$. Known from *Coriolus versicolor* only.

Discussion. This species and the closely related *C. corticinus* Gorham from the Mexican highlands both prefer the fruiting bodies of *Coriolus versicolor* and its relatives.

34. *Cis tridentatus* Mannerheim

Geographical range. Pacific Coast from southern Alaska to Monterey County, California.

Host range. Fungi: 9(6). Records: 19 (12). $B_s = 3.46$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Pleurotus ostreatus	1	0	1	0.0
Poria carbonica	0	1	1	8.3
Laetiporus sulphureus	0	1	1	8.3
Tyromyces cinerascens	1	1	2	8.3
Fomitopsis pinicola	3	7	10	58.3
Antrodia sepium	0	1	1	8.3
Ganoderma applanatum	1	0	1	0.0
Ganoderma oregonense	0	1	1	8.3
Phellinus gilvus	1	0	1	0.0
Totals	7	12	19	100.0

Discussion. This is a member of the *Cis americanus* complex and is restricted to the Pacific Coast (*see* p. 189). It is usually found in *Fomitopsis pinicola* where it may coexist with *Cis biarmatus* and *Dolichocis indistinctus.*

35. *Cis tristis* Mellié

Geographical range. Eastern North America, from New York and Massachusetts south to Florida and west as far as southeastern Colorado and northeastern Mexico.

Host range. Fungi: 9(5). Records: 14 (7). $B_s = 4.36$. $B_g = 2.57$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Pleurotus sp.	1	0	1	0.0
Fomitella supina	2	0	2	0.0
Pycnoporus cinnabarinus	1	0	1	0.0
Coriolus hirsutus	2	0	2	0.0
Coriolus maximus	0	1	1	14.3
Coriolus versicolor	0	3	3	42.9
Lenzites betulina	1	1	2	14.3
Lenzites elegans	0	1	1	14.3
Funalia hispida	0	1	1	14.3
Totals	7	7	14	100.0

36. *Cis ursulinus* Casey

Geographical range. Southeastern United States, from North Carolina south to Florida and west to Arkansas and Louisiana.

Host range. Fungi: 5(0). Records: 5 (0).

Records.	NB	BR	TOT	%BR
Laetiporus sulphureus	1	0	1	0.0
Bjerkandera adusta	1	0	1	0.0
Hirschioporus versatilis	1	0	1	0.0
Ganoderma tsugae	1	0	1	0.0
Phellinus gilvus	1	0	1	0.0
Totals	5	0	5	0.0

37. *Cis versicolor* Casey

Geographical range. Extreme southern Oregon, south throughout most of California west of the Sierran crest, into Baja California Norte and east through Arizona into New Mexico and western Texas.

Host range. Fungi: 7(4). Records: 40 (23). $B_s = 2.78$. $B_g = 2.18$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Schizophyllum commune	1	0	1	0.0
Pycnoporus cinnabarinus	1	0	1	0.0
Coriolus hirsutus	3	2	5	8.7
Coriolus versicolor	8	15	23	65.2
Lenzites betulina	0	2	2	8.7
Funalia hispida	3	4	7	17.4
Ganoderma brownii	1	0	1	0.0
Totals	17	23	40	100.0

Discussion. Cis versicolor is a relatively common species throughout the Southwest in both mesic (central California coast) and xeric (California and Arizona deserts) environments.

38. *Cis vitulus* Mannerheim

Geographical range. California, from Del Norte County to San Diego County, and north-central Arizona.

Host range. Fungi: 4(3). Records: 36 (22). $B_s = 1.78$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Schizophyllum commune	1	0	1	0.0
Bjerkandera adusta	1	1	2	4.6
Coriolus versicolor	11	18	29	81.8
Lenzites betulina	1	3	4	13.6
Totals	14	22	36	100.0

Discussion. This species belongs to a Neotropical group including the southeastern *C. congestus,* the Mexican *C. bubalus* Reitter, and the Central American *C. fasciatus* Gorham. In California, it breeds primarily on *Coriolus versicolor* in mesic situations, where it may be associated with *Cis fuscipes, C. versicolor, Sulcacis curtulus,* and *Octotemnus laevis.* Other tropical members of the group have been collected in *C. versicolor* and *C. pinisitus* (Lawrence, unpublished data).

39. *Ennearthron aurisquamosum* Lawrence

Geographical range. Kentucky and North Carolina.

Host range. Fungi: 1(0). Records: 1 (0). Known from *Bjerkandera adusta* only.

Discussion. This is an isolated species whose closest relatives occur in eastern Asia; it is apparently rare. An undescribed relative from western China was collected in a herbarium specimen of *Cryptoporus volvatus* (Lawrence, unpublished data).

40. *Ennearthron spenceri* (Hatch)

Geographical range. Known only from Vancouver, British Columbia. Probably introduced from Japan.

Host range. Known from *Cryptoporus volvatus* only.

Records. A single unverified record from *C. volvatus*.

Discussion. It is not known that this species occurs naturally in British Columbia. The records do not make it clear whether the infested specimens of *Cryptoporus volvatus* were sent from Japan or taken locally. The species most closely related to *E. spenceri* are all Japanese.

41. *Dolichocis indistinctus* Hatch

Geographical range. Known from scattered localities throughout the northern and montane parts of North America, from the northern coast of British Columbia to the Gaspé Peninsula of Quebec and south into the Sierra Nevada, Chiricahua Mountains of southern Arizona, and Green Mountains of Vermont.

Host range. Fungi: 3(1). Records: 9 (5). $B_s = 1.95$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Laricifomes officinalis	1	0	1	0.0
Fomitopsis pinicola	3	3	6	60.0
Antrodia serialis	0	2	2	40.0
Totals	4	5	9	100.0

Discussion. This is the North American counterpart of the European *D. laricinum* (Mellié) and the two are doubtfully distinct. It is most commonly taken in *Fomitopsis pinicola* along the Pacific Coast, while its Palaearctic sibling has been recorded from the same fungus in Scandinavia (Saalas, 1923).

42. *Dolichocis manitoba* Dury

Geographical range. Northern and montane regions of North America, from the northern coast of British Columbia to New Brunswick and south to the central California coast, southern Sierra Nevada, southeastern Utah, and northern Pennsylvania.

Host range. Fungi: 12(7). Records: 73 (31). $B_s = 2.95$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Laetiporus sulphureus	0	1	1	3.2
Bjerkandera adusta	2	0	2	0.0
Piptoporus betulinus	2	3	5	9.7
Cryptoporus volvatus	1	0	1	0.0
Laricifomes officinalis	0	1	1	3.2
Fomitopsis pinicola	29	22	51	71.0
Heterobasidion annosum	1	2	3	6.5
Irpex tulipiferae	1	0	1	0.0
Hirschioporus pargamenus	4	0	4	0.0
Cerrena unicolor	1	1	2	3.2
Fomes fomentarius	1	0	1	0.0
Ganoderma applanatum	0	1	1	3.2
Totals	42	31	73	100.0

Discussion. In western North America, this is a common and characteristic inhabitant of *Fomitopsis pinicola,* while in the Northeast it occurs in association with several other fungi, including *Piptoporus betulinus, Fomes fomentarius,* and *Cerrena unicolor.* Matthewman and Pielou (1971), in their study of arthropods associated with *F. fomentarius* in Quebec (data not included above), found that *D. manitoba* was less common than *Cis levettei* but still capable of causing considerable damage to sporophores. This is one of the few ciids in which there is an apparent change in host preference with geographic area (*see* p. 189). This may be connected with floristic change, since *F. fomentarius* and *P. betulinus* are much less common in the western coniferous forests, but it may also be an indication that *D. manitoba* has more recently colonized the eastern part of the continent.

43. *Orthocis punctatus* (Mellié)

Geographical range. Widespread across North America from the edge of the Beaufort Sea (Mackenzie District, Northwest Territory) to the island of Newfoundland, south on the Pacific Coast to Santa Barbara, California, through the Rocky Mountains to northeastern New Mexico, into the Black Hills of South Dakota, and through the eastern and midwestern states from New England to Florida and west to Kansas and Texas.

Host range. Fungi: 1(1). Records: 1 (1). Known from *Auricularia auricula* only.

Discussion. As mentioned in an earlier paper (Lawrence, 1971), this species may represent a complex of two or more related forms. The single record from *Auricularia auricula* is from coastal North Carolina (Atlantic Beach) and represents the southern form rather than the typical *O. punctatus.* Among the Palaearctic species of *Orthocis, O. coluber* (Abeille) has been collected in *Auricularia auricula* (Falcoz, 1922), while *O. alni* (Gyllenhal) is known from *A. auricula, Stereum rugosum,* and the tremellaceous *Exidia glandulosa* (Benick, 1952). In Panama, an undescribed *Orthocis* appears to be common in *Auricularia polytricha* (Lawrence, unpublished data).

44. *Strigocis bilimeki* (Reitter)

Geographical range. Mountains of northern Mexico; probably extending into southern Arizona.

Host range. Fungi: 2(1). Records: 2 (1). Group: *Coriolus*?

Records.	NB	BR	TOT	%BR
Coriolus versicolor	1	0	1	0.0
Lenzites betulina	0	1	1	100.0
Totals	1	1	2	100.0

45. *Strigocis opacicollis* Dury

Geographical range. Eastern North America, from southern Vermont and New Hampshire to the Florida Keys, west as far as eastern Kansas, and south into Mexico.

Host range. Fungi: 10(5). Records: 48 (18). $B_s = 2.29$. $B_g = 1.23$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Bjerkandera adusta	1	0	1	0.0
Pycnoporus sanguineus	1	0	1	0.0
Coriolus hirsutus	5	0	5	0.0
Coriolus maximus	0	1	1	5.6
Coriolus pinisitus	0	1	1	5.6
Coriolus subectypus	0	1	1	5.6
Coriolus tenuis	1	0	1	0.0
Coriolus versicolor	15	14	29	77.8
Lenzites betulina	6	1	7	5.6
Phellinus gilvus	1	0	1	0.0
Totals	30	18	48	100.0

Discussion. Strigocis opacicollis is a fairly common inhabitant of *Coriolus versicolor* and its relatives in eastern North America. The European member of this genus, *S. bicornis* (Mellié), is known to breed in the same fungus, as well as *Pseudotrametes gibbosa* (Paviour-Smith, 1960a, 1969; Peyerimhoff, 1915; Roman, 1970). Other New World species, such as *S. opalescens* and *S. bilimeki,* have a similar preference for members of the *Coriolus* group.

46. *Strigocis opalescens* (Casey)

Geographical range. Eastern North America, from southern Michigan and New York south and west as far as northeastern Mexico.

Host range. Fungi: 1(1). Records: 3 (1). Known from *Coriolus versicolor* only.

47. *Hadraule blaisdelli* (Casey)

Geographical range. Western North America, from southern British Columbia to southern California, east through Utah, Arizona, and New Mexico into Texas, and south into Mexico. Also known from Michigan, Iowa, Ohio, Connecticut, Massachusetts, and Florida, but all but the first represent herbarium infestations.

Host range. Fungi: 11(7). Records: 19 (8). $B_s = 6.77$.

Records.	NB	BR	TOT	%BR
Bjerkandera adusta	2	1	3	12.5
Heterobasidion annosum	0	1	1	12.5
Antrodia sepium	3	0	3	0.0

Dichomitus squalens	0	1	1	12.5
Coriolus biformis	0	1	1	12.5
Coriolus versicolor	2	0	2	0.0
Funalia hispida	0	1	1	12.5
Gloeophyllum saepiarium	1	2	3	25.0
Daedaleopsis confragosa	0	1	1	12.5
Inonotus munzii	2	0	2	0.0
Phellinus robiniae	1	0	1	0.0
Totals	11	8	19	100.0

Discussion. This species has a relatively broad host range and it is difficult to determine from existing records if it does prefer one group of fungi. This is the only ciid known to infest herbarium fungus collections (Lawrence, 1971).

48. *Hadraule elongatula* (Gyllenhal)

Geographical range. In North America, known only from New Brunswick. In the Old World, widespread throughout Europe, North Africa, and Siberia.

Host range. Fungi: 1(1). Records: 1 (1). Known from *Piptoporus betulinus* only.

Discussion. It is not known whether the New Brunswick population represents a single introduction from Europe or whether this species is more widespread in northern North America. Palm (1946) has reported *H. elongatula* from a birch fungus in Scandinavia, while all other records for the species are from under bark, in rotten wood, or in the galleries of other beetles (*see* Lawrence, 1971).

49. *Plesiocis cribrum* Casey

Geographical range. Northern and montane regions of North America (particularly the western part), from British Columbia to the Gaspé Peninsula of Quebec, south to the Laguna Mountains in California, the edge of the Colorado Plateau in Arizona and New Mexico, the Great Lakes region, and the Shenandoah Mountains of Virginia.

Host range. Fungi: 3(2). Records: 58 (35). $B_s = 1.51$.

Records.	NB	BR	TOT	%BR
Hapalopilus alboluteus	2	0	2	0.0
Cryptoporus volvatus	18	30	48	85.7
Dichomitus squalens	3	5	8	14.3
Totals	23	35	58	100.0

Discussion. This species is extremely common in *Cryptoporus volvatus* and is also known to breed in *Dichomitus squalens*. If the somewhat doubtful records for *Cis laminatus* and *Ennearthron spenceri* are disregarded, *Plesiocis cribrum* is the only North American ciid known to breed in the fruiting bodies of *C. volvatus* (*see* p. 187).

50. *Ceracis californicus* (Casey)

Geographical range. Western North America, from Seattle, Washington, east to western Nebraska, south along the Pacific Coast to southern California, through the Great Basin and Rocky Mountains to southern Arizona and New Mexico, and south in Mexico as far as Baja California Sur and southern Sinaloa.

Host range. Fungi: 20(15). Records: 80(32). $B_s = 11.20$. $B_g = 5.89$. Group: *Ganoderma*?

Records.	NB	BR	TOT	%BR
Pleurotus ostreatus	2	1	3	3.1
Steccherinum ochraceum	2	1	3	3.1
Poria versipora	1	1	2	3.1
Bjerkandera adusta	9	2	11	6.3
Fomitopsis cajanderi	1	0	1	0.0
Fomitopsis fraxinophilus	0	1	1	3.1
Heterobasidion annosum	0	1	1	3.1
Hirschioporus pargamenus	0	1	1	3.1
Cerrena unicolor	0	1	1	3.1
Coriolus versicolor	19	5	24	15.6
Lenzites betulina	5	0	5	0.0
Funalia hispida	2	2	4	6.3
Datronia mollis	1	0	1	0.0
Ganoderma applanatum	0	2	2	6.3
Ganoderma brownii	2	8	10	25.0
Ganoderma lobatum	0	3	3	9.4
Ganoderma lucidum	0	1	1	3.1
Ganoderma oregonense	1	0	1	0.0
Ganoderma sp.	1	2	3	6.3
Phellinus gilvus	2	0	2	0.0
Totals	48	32	80	100.0

Discussion. Ceracis californicus has a relatively broad host range, including breeding records for at least 15 fungi. There is some indication that it prefers the conks of various *Ganoderma*, especially towards the center of its geographical range (Arizona and northern Mexico), while its apparent preference for *Coriolus versicolor* in northern California is partly due to the abundance of that particular host.

51. *Ceracis curtus* (Mellié)

Geographical range. Southeastern United States, from Florida to south-central Texas, the Bahamas, and the Greater Antilles.

Host range. Fungi: 2(1). Records: 4 (2). Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Pogonomyces hydnoides	1	2	3	100.0
Fomes sclerodermeus	1	0	1	0.0
Totals	2	2	4	100.0

52. *Ceracis dixiensis* (Tanner)

Geographical range. Southwestern North America, from southern Utah to Guadalajara, Mexico, and from the Colorado River in California to the Big Bend Region in Texas.

Host range. Fungi: 2(1). Records: 12 (9). $B_s = 1.00$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Funalia hispida	2	9	11	100.0
Ganoderma sp.	1	0	1	0.0
Totals	3	9	12	100.0

Discussion. In southwestern North America, this species is commonly found in the sporophores of *Funalia hispida* on cottonwoods (*Populus* sp.) growing along river beds. It is often associated with *Cis versicolor.*

53. *Ceracis magister* Lawrence

Geographical range. Known only from Lignum Vitae Key, Florida.

Host range. Fungi: 1(1). Records: 4 (4). Known from *Phellinus robiniae* only.

54. *Ceracis minutissimus* (Mellié)

Geographical range. Eastern United States, from New Hampshire and Michigan to Alabama.

Host range. Fungi: 3(1). Records: 11 (9). $B_s = 1.00$.

Records.	NB	BR	TOT	%BR
Bjerkandera adusta	1	0	1	0.0
Cerrena unicolor	0	9	9	100.0
Coriolus versicolor	1	0	1	0.0
Totals	2	9	11	100.0

Discussion. This species is most common in the Northeast where it breeds exclusively on *Cerrena unicolor.*

55. *Ceracis minutus* Dury

Geographical range. Southern Texas, Florida, the Bahamas, and the Greater Antilles.

Host range. Fungi: 9(8). Records: 34 (24). $B_s = 7.09$. Group: *Coriolus*?

Records.	NB	BR	TOT	%BR
Lopharia papyrina	2	3	5	12.5
Pycnoporus sanguineus	0	3	3	12.5
Coriolus maximus	0	3	3	12.5
Coriolus pinisitus	4	6	10	25.0
Lenzites elegans	0	1	1	4.2
Earliella corrugata	0	1	1	4.2
Coriolopsis occidentalis	0	3	3	12.5
Pogonomyces hydnoides	3	4	7	16.7
Fomes sclerodermeus	1	0	1	0.0
Totals	10	24	34	100.0

Discussion. Ceracis minutus is another species with a broad host range and no apparent preference for one group of fungi. Most of the records, however, are from the Florida Keys, and several ciids appear to be more polyphagous in this area (*see* p. 189).

56. *Ceracis monocerus* Lawrence

Geographical range. Florida, Louisiana, and Cuba.

Host range. Fungi: 1(1). Records: 2 (1). Known from *Pycnoporus sanguineus* only.

Discussion. This southeastern species is known only from *Pycnoporus sanguineus,* but its Neotropical relatives, such as *Ceracis furcifer* Mellié and *C. ruficornis* (Pic), are known from various *Coriolus* and *Lenzites* as well.

57. *Ceracis multipunctatus* (Mellié)

Geographical range. Alabama, Florida, Cuba, Jamaica, and Montserrat.

Host range. Fungi: 6(3). Records: 17 (13). $B_s = 2.95$. $B_g = 1.99$. Group: *Ganoderma*.

Records.	NB	BR	TOT	%BR
Fomitella supina	1	0	1	0.0
Pogonomyces hydnoides	1	0	1	0.0
Fomes sclerodermeus	0	4	4	30.8
Ganoderma applanatum	0	4	4	30.8
Ganoderma lucidum	1	0	1	0.0
Ganoderma zonatum	1	5	6	38.5
Totals	4	13	17	100.0

Discussion. This is one of several southeastern and Neotropical *Ceracis* with a preference for *Fomes* and *Ganoderma*. In Florida, it is commonly associated with *Cis hirsutus* and *Ceracis punctulatus*.

58. *Ceracis nigropunctatus* Lawrence

Geographical range. Louisiana and Texas south, through Mexico and Central America, to Panama.

Host range. Fungi: 4(2). Records: 14 (5). $B_s = 1.66$. Group: *Ganoderma*.

Records.	NB	BR	TOT	%BR
Coriolus hirsutus	2	0	2	0.0
Pogonomyces hydnoides	5	4	9	80.0
Fomes sclerodermeus	0	1	1	20.0
Ganoderma sp.	2	0	2	0.0
Totals	9	5	14	100.0

59. *Ceracis obrieni* Lawrence

Geographical range. Southeastern Arizona and southern Sinaloa, Mexico.

Host range. Fungi: 1(1). Records: 5 (5). $B_s = 1.00$. Known from *Phellinus gilvus* only.

Discussion. This is the only member of the southwestern fauna to breed in *Phellinus gilvus*, which harbors many species in the Southeast and tropical America.

60. *Ceracis pecki* Lawrence

Geographical range. Eastern United States, from Illinois and Maryland south to Florida.

Host range. Fungi: 1(1). Records: 1 (1). Known from *Melanoporia nigra* only.

61. *Ceracis powelli* Lawrence

Geographical range. Southeastern Arizona and southern Durango, Mexico.

Host range. Fungi: 2(1). Records: 3 (1). Group: *Hirschioporus*.

Records.	NB	BR	TOT	%BR
Hirschioporus abietinus	1	1	2	100.0
Hirschioporus pargamenus	1	0	1	0.0
Totals	2	1	3	100.0

Discussion. *Ceracis powelli* is the only species of *Ceracis* known to breed exclusively in *Hirschioporus*, although *C. thoracicornis* is commonly found in these fruiting bodies.

62. *Ceracis pullulus* (Casey)

Geographical range. Southeastern United States, from North Carolina to Florida and west to Louisiana, the Greater Antilles, and the Virgin Islands.

Host range. Fungi: 10(7). Records: 43 (23). $B_s = 5.13$. $B_g = 3.09$. Group: *Phellinus*.

Records.	NB	BR	TOT	%BR
Nigroporus vinosus	1	0	1	0.0
Pogonomyces hydnoides	2	0	2	0.0
Ganoderma zonatum	2	2	4	8.7
Cyclomyces iodinus	1	1	2	4.3
Inonotus corrosus	0	1	1	4.3
Inonotus porrectus	0	4	4	17.4
Inonotus sp.	1	0	1	0.0
Melanoporia nigra	0	1	1	4.3
Phellinus gilvus	12	8	20	34.8
Phellinus licnoides	1	6	7	26.1
Totals	20	23	43	100.0

Discussion. This species and the related *C. singularis* have an obvious preference for xanthochroic fruiting bodies, especially those of *Phellinus*.

63. *Ceracis punctulatus* Casey

Geographical range. Eastern United States (east of the 100th meridian), from Michigan and southern Vermont to southern Texas and the Florida Keys, Cuba, and Jamaica.

Host range. Fungi: 19(9). Records: 92

(45). $B_s = 4.26$. $B_g = 2.88$. Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Stereum ostrea	1	0	1	0.0
Lopharia papyrina	0	2	2	4.4
Bjerkandera adusta	1	0	1	0.0
Hirschioporus pargamenus	1	0	1	0.0
Pycnoporus sanguineus	2	0	2	0.0
Coriolus pinisitus	1	0	1	0.0
Earliella corrugata	1	0	1	0.0
Coriolopsis fulvocinerea	1	2	3	4.4
Pogonomyces hydnoides	9	9	18	20.0
Fomes fomentarius	1	0	1	0.0
Ganoderma curtisii	1	0	1	0.0
Ganoderma lucidum	1	0	1	0.0
Ganoderma zonatum	2	1	3	2.2
Ganoderma sp.	1	0	1	0.0
Inonotus porrectus	0	1	1	2.2
Inonotus sp.	0	1	1	2.2
Phellinus gilvus	21	25	46	55.6
Phellinus licnoides	0	2	2	4.4
Phellinus robiniae	3	2	5	4.4
Totals	47	45	92	100.0

Discussion. Throughout most of its range, *Ceracis punctulatus* breeds in the sporophores of *Phellinus gilvus.* In Florida, however, the species is more variable in color (*see* Lawrence, 1967b) and has a broader host range, including *Pogonomyces hydnoides, Coriolopsis fulvocinerea,* and *Lopharia papyrina.* This may be tied in with the relatively recent disruption of the Floridian fauna, owing to Pleistocene flooding, and also to the constant immigration of Caribbean forms through the action of hurricanes (*see* p. 189). In the middle and northern parts of the range, the species is a characteristic inhabitant of *P. gilvus,* while the closely related *C. sallei* occurs in *Ganoderma applanatum.*

64. *Ceracis quadricornis* Gorham

Geographical range. Southern Texas through eastern and southern Mexico and as far south as Costa Rica.

Host range. Fungi: 7(5). Records: 21 (13). $B_s = 4.26$. Group: *Coriolus*?

Records.	NB	BR	TOT	%BR
Trametes cirrifer	1	0	1	0.0
Coriolus hirsutus	1	1	2	7.7
Coriolus maximus	1	3	4	23.1
Earliella corrugata	0	1	1	7.7
Coriolopsis crocata	1	0	1	0.0
Coriolopsis occidentalis	3	4	7	30.8
Pogonomyces hydnoides	1	4	5	30.8
Totals	8	13	21	100.0

65. *Ceracis sallei* Mellié

Geographical range. Eastern North America, from southern Ontario and Quebec to southern Texas and Florida, east of the 100th meridian.

Host range. Fungi: 10(6). Records: 45 (22). $B_s = 2.45$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Oxyporus populinus	0	1	1	4.5
Fomitopsis pinicola	1	0	1	0.0
Pycnoporus cinnabarinus	1	0	1	0.0
Pogonomyces hydnoides	1	1	2	4.5
Fomes sclerodermeus	1	0	1	0.0
Ganoderma applanatum	15	17	32	77.3
Ganoderma curtisii	2	1	3	4.5
Ganoderma lobatum	0	1	1	4.5
Ganoderma zonatum	1	1	2	4.5
Ganoderma sp.	1	0	1	0.0
Totals	23	22	45	100.0

Discussion. This species is almost entirely restricted to the fruiting bodies of *Ganoderma applanatum* and its relatives and usually occurs in association with *Cis levettei* in the Northeast.

66. *Ceracis schaefferi* Dury

Geographical range. Southern Texas and eastern Mexico.

Host range. Known from *Ganoderma* sp. only.

Records. A single unverified record from "*Ganoderma pseudoboletus.*"

67. *Ceracis similis* Horn

Geographical range. Baja California Sur and Nayarit, Mexico, south to El Salvador.

Host range. Fungi: 3(3). Records: 6 (6). $B_s = 2.78$. $B_g = 1.00$. Group: *Ganoderma.*

Records.	NB	BR	TOT	%BR
Ganoderma applanatum	0	1	1	16.7
Ganoderma zonatum	0	3	3	50.0
Ganoderma sp.	0	2	2	33.3
Totals	0	6	6	100.0

68. *Ceracis singularis* (Dury)

Geographical range. Eastern North America, from northern Minnesota and Massachusetts to southern Texas and Louisiana; a single record from Mt. Irazu in Costa Rica.

Host range. Fungi: 21(9). Records: 59 (17). $B_s = 6.45$. $B_g = 2.40$. Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Fomitella supina	1	0	1	0.0
Heterobasidion annosum	1	0	1	0.0
Hirschioporus pargamenus	2	0	2	0.0
Trametes plebeja	1	0	1	0.0
Coriolus versicolor	1	0	1	0.0
Funalia hispida	1	0	1	0.0
Gloeophyllum saepiarium	0	1	1	5.9
Daedaleopsis confragosa	1	0	1	0.0
Fomes sclerodermeus	2	0	2	0.0
Ganoderma applanatum	6	2	8	11.8
Ganoderma curtisii	1	1	2	5.9
Ganoderma tsugae	1	0	1	0.0
Ganoderma sp.	1	0	1	0.0
Inonotus sp.	2	0	2	0.0
Melanoporia nigra	1	1	2	5.9
Phellinus gilvus	14	7	21	41.2
Phellinus igniarius	1	1	2	5.9
Phellinus licnoides	1	0	1	0.0
Phellinus ribis	0	1	1	5.9
Phellinus robiniae	4	2	6	11.8
Phellinus sp.	0	1	1	5.9
Totals	42	17	59	100.0

Discussion. Ceracis singularis is found throughout eastern North America but is particularly common in the Midwest. It is one of the few Nearctic ciids which breeds in the woody conks of *Phellinus robiniae* and *P. igniarius.*

69. *Ceracis thoracicornis* (Ziegler)

Geographical range. Eastern North America, from southeastern Manitoba and southern Quebec to southern Texas and Florida.

Host range. Fungi: 36(21). Records: 187(73). $B_s = 12.00$. $B_g = 8.31$. Group: *Hirschioporus?*

Records.	NB	BR	TOT	%BR
Boletus sp.	1	0	1	0.0
Stereum ostrea	2	0	2	0.0
Polyporus squamosus	1	2	3	2.7
Gloeoporus dichrous	1	0	1	0.0
Laetiporus sulphureus	1	0	1	0.0
Tyromyces spraguei	0	1	1	1.4
Bjerkandera adusta	9	7	16	9.6
Nigroporus vinosus	1	0	1	0.0
Fomitella supina	10	15	25	20.5
Fomitopsis fraxineus	1	0	1	0.0
Fomitopsis pinicola	1	0	1	0.0
Rigidoporus ulmarius	5	1	6	1.4
Rigidoporus vitreus	0	1	1	1.4
Irpex tulipiferae	0	1	1	1.4
Hirschioporus abietinus	2	1	3	1.4
Hirschioporus pargamenus	26	16	42	21.9
Hirschioporus sector	4	2	6	2.7
Cerrena unicolor	4	2	6	2.7
Trametes plebeja	2	0	2	0.0
Pycnoporus cinnabarinus	1	0	1	0.0
Coriolus hirsutus	3	1	4	1.4
Coriolus versicolor	8	3	11	4.1
Lenzites betulina	4	6	10	8.2
Lenzites elegans	3	7	10	9.6
Earliella corrugata	1	1	2	1.4
Funalia hispida	0	1	1	1.4
Funalia trogii	0	1	1	1.4
Pogonomyces hydnoides	1	0	1	0.0
Fomes fomentarius	2	0	2	0.0
Fomes sclerodermeus	1	1	2	1.4
Ganoderma applanatum	7	0	7	0.0
Ganoderma curtisii	1	0	1	0.0
Ganoderma lucidum	3	2	5	2.7
Ganoderma tsugae	4	1	5	1.4
Ganoderma sp.	1	0	1	0.0
Phellinus gilvus	3	0	3	0.0
Totals	114	73	187	100.0

Discussion. This is another eurytrophic species whose host range is almost as broad as that of *Cis americanus.* There is some indication of a preference for *Hirschioporus,* but there are also numerous records for *Coriolus, Lenzites,* and *Fomitella supina.* The number of records for the last may represent an artifact resulting from the abundance of that particular fungus in Florida and Louisiana. In spite of the large number of host fungi for this species, there is a notable absence of breeding records for members of the Hymenochaetaceae.

70. *Sulcacis curtulus* (Casey)

Geographical range. Northern and montane regions of North America, from British Columbia to southern Quebec and New England, south to San Diego County, California, the mountains of southern Arizona and northern Mexico, and the states of Nebraska, Illinois, and North Carolina.

Host range. Fungi: 14(7). Records: 119(55). $B_s = 3.46$. $B_g = 2.51$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Pleurotus ostreatus	3	0	3	0.0
Schizophyllum commune	0	1	1	1.8
Stereum hirsutum	1	0	1	0.0
Steccherinum ochraceum	1	0	1	0.0
Bjerkandera adusta	8	3	11	5.5
Pycnoporus cinnabarinus	1	1	2	1.8
Coriolus hirsutus	6	6	12	10.9
Coriolus versicolor	34	35	69	63.6
Lenzites betulina	3	5	8	9.1
Funalia hispida	2	4	6	7.3
Ganoderma applanatum	1	0	1	0.0
Inonotus rheades	1	0	1	0.0
Phellinus gilvus	1	0	1	0.0
Phellinus igniarius	2	0	2	0.0
Totals	64	55	119	100.0

Discussion. This is primarily a western species, although it does occur in the Northeast as well. It is a fairly common inhabitant of *Coriolus versicolor* and its relatives on the Pacific Coast. It appears to be closely related to the Palaearctic *Sulcacis bidentulus* (Rosenhauer), which has been recorded from *Funalia extenuata* (probably the same as *F. hispida*) and from *F. trogii* (Peyerimhoff, 1915; Roman, 1970). Other members of the genus, such as *S. affinis* (Gyllenhal) and *S. fronticornis* (Panzer), usually prefer members of the *Coriolus* group (Benick, 1952; Falcoz, 1921; Roman, 1970; Saalas, 1923; Scheerpletz and Höfler, 1948).

71. *Sulcacis lengi* Dury

Geographical range. Eastern North America, from Maine to the Carolinas and west to eastern Kansas and Texas.

Host range. Fungi: 5(3). Records: 20 (7). $B_s = 2.95$. Group: *Coriolus.*

Records.	NB	BR	TOT	%BR
Boletus sp.	1	0	1	0.0
Coriolus hirsutus	1	0	1	0.0
Coriolus pubescens	0	2	2	28.6
Coriolus versicolor	8	3	11	42.8
Lenzites betulina	3	2	5	28.6
Totals	13	7	20	100.0

72. *Malacocis brevicollis* (Casey)

Geographical range. Eastern North America, from northern Maine to the Florida Keys and west to southern Manitoba, eastern Kansas, and Texas.

Host range. Fungi: 16(9). Records: 79 (37). $B_s = 5.50$. $B_g = 1.12$. Group: *Phellinus.*

Records.	NB	BR	TOT	%BR
Nigroporus vinosus	1	0	1	0.0
Pogonomyces hydnoides	1	0	1	0.0
Fomes fomentarius	1	0	1	0.0
Inonotus corrosus	0	1	1	2.7
Phellinus everhartii	1	1	2	2.7
Phellinus ferruginosus	1	0	1	0.0
Phellinus gilvus	20	16	36	43.2
Phellinus igniarius	5	8	13	21.6
Phellinus johnsonianus	1	0	1	0.0
Phellinus laevigatus	1	3	4	8.1
Phellinus licnoides	3	0	3	0.0
Phellinus pini	0	1	1	2.7
Phellinus pomaceus	1	0	1	0.0
Phellinus robiniae	4	3	7	8.1
Phellinus robustus	2	2	4	5.4
Phellinus sp.	0	2	2	5.4
Totals	42	37	79	100.0

Discussion. *Malacocis brevicollis* breeds only in the darker hymenochaetoid fungi and is the most common inhabitant of *Phellinus robiniae* and *P. igniarius* throughout eastern North America. Several undescribed *Malacocis* in Central America have similar preferences.

73. *Rhopalodontus americanus* Lawrence

Geographical range. Known only from northern Wisconsin.

Host range. Fungi: 3(1). Records: 3 (1). Group: *Ganoderma*?

Records.	NB	BR	TOT	%BR
Russula sp.	1	0	1	0.0
Hapalopilus fibrillosus	1	0	1	0.0
Piptoporus betulinus	0	1	1	100.0
Totals	2	1	3	100.0

Discussion. This is the only New World representative of the Eurasian genus *Rhopalodontus.* Its European relative *R. perforatus* (Gyllenhal) has been recorded as breeding in *Fomes fomentarius* and *Piptoporus betulinus* (Benick, 1952; Paviour-Smith, 1969; Saalas, 1923).

74. *Octotemnus laevis* Casey

Geographical range. Northern part of North America, from southern Alaska to Quebec and Nova Scotia, south along the Pacific Coast to Monterey County, California, in the Sierra Nevada to Tulare County, in the Midwest to southern Iowa and Kansas, and on the East Coast to Alabama.

Host range. Fungi: 14(6). Records: 130(63). $B_s = 2.24$. $B_g = 1.26$. Group: *Coriolus.*

Records.	NB	BR	TOT	% BR
Stereum sp.	1	0	1	0.0
Polyporus squamosus	1	0	1	0.0
Laetiporus sulphureus	1	0	1	0.0
Tyromyces albellus	1	0	1	0.0
Tyromyces galactinus	1	0	1	0.0
Bjerkandera adusta	1	0	1	0.0
Hirschioporus abietinus	1	0	1	0.0
Hirschioporus pargamenus	1	0	1	0.0
Coriolus conchifer	1	4	5	6.3
Coriolus hirsutus	10	1	11	1.6
Coriolus pubescens	3	5	8	7.9
Coriolus versicolor	37	50	87	79.4
Lenzites betulina	4	2	6	3.2
Ganoderma applanatum	4	1	5	1.6
Totals	67	63	130	100.0

Discussion. This is an extremely common species throughout the northern part of North America, where it breeds almost exclusively on *Coriolus versicolor* and its relatives. It is only doubtfully distinct from the Palaearctic *O. glabriculus* (Gyllenhal), which is known to have similar host preferences, being most commonly recorded as breeding in *C. versicolor, C. hirsutus, Lenzites betulina,* and *Pseudotrametes gibbosa* (Benick, 1952; Donisthorpe, 1935; Falcoz, 1921; Paviour-Smith, 1960a; Roman, 1970; Scheerpeltz and Höfler, 1948).

HOST FUNGI AND ASSOCIATED CIIDAE

For each fungus species below, the total number of records and number of breeding records (in parentheses) are given, and these are followed by a list of ciid species known to breed in the sporophores (BR) and those known from nonbreeding records only (NB). To conserve space, each ciid species is represented by its corresponding number in Table 1.

Auricularia auricula. 1(1). BR: 43.
Auricularia polytricha. 1(0). NB: 17.
Lentinus crinitus. 1(0). NB: 5.
Panellus stipticus. 1(1). BR: 31.
Pleurotus ostreatus. 10(2). BR: 2, 50. NB: 34, 70.
Pleurotus sp. 2(0). NB: 10, 35.
Schizophyllum commune. 4(1). BR: 70. NB: 10, 37, 38.
Boletus sp. 2(0). NB: 69, 71.
Russula sp. 1(0). NB: 73.
Phlebia merismoides. 1(0). NB: 2.
Stereum hirsutum. 7(4). BR: 2. NB: 70.
Stereum ostrea. 20(5). BR: 29. NB: 5, 21, 24, 28, 32, 63, 69.
Stereum sp. 3(2). BR: 29. NB: 74.
Lopharia papyrina. 12(7). BR: 11, 55, 63.
Steccherinum ochraceum. 7(3). BR: 2, 50. NB: 70
Poria carbonica. 1(1). BR: 34.
Poria corticola. 1(1). BR: 10.
Poria versipora. 7(3). BR: 2, 50. NB: 14, 19.
Polyporus mutabilis. 1(1). BR: 5.
Polyporus squamosus. 9(5). BR: 2, 16, 69. NB: 21, 74.
Gloeoporus dichrous. 1(0). NB: 69.
Hapalopilus alboluteus. 2(0). NB: 49.
Hapalopilus fibrillosus. 1(0). NB: 73.
Laetiporus sulphureus. 11(3). BR: 2, 34, 42. NB: 10, 14, 23, 36, 69, 74.
Tyromyces albellus. 1(0). NB: 74.
Tyromyces cinerascens. 3(1). BR: 34. NB: 19.
Tyromyces galactinus. 1(0). NB: 74.
Tyromyces spraguei. 1(1). BR: 69.
Bjerkandera adusta. 77(27). BR: 2, 5, 10, 16, 26, 38, 47, 50, 69, 70. NB: 21, 32, 36, 39, 42, 45, 54, 63, 74.
Oxyporus latemarginatus. 3(1). BR: 10. NB: 5.
Oxyporus populinus. 5(4). BR: 21, 65.

Ischnoderma resinosum. 3(2). BR: 2, 21. NB: 14.
Nigroporus vinosus. 4(1). BR: 5. NB: 62, 69, 72.
Fomitella supina. 32(15). BR: 69. NB: 10, 17, 24, 35, 57, 68.
Piptoporus betulinus. 17(10). BR: 2, 21, 42, 48, 73. NB: 14.
Cryptoporus volvatus. 49(30) + 2 unverified. BR: 49. NB: 42. Unverified: 20, 40.
Laricifomes officinalis. 7(5). BR: 10, 13, 42. NB: 3, 41.
Fomitopsis cajanderi. 4(3). BR: 12. NB: 50.
Fomitopsis fraxinea. 2(0). NB: 16, 69.
Fomitopsis fraxinophila. 1(1). BR: 50.
Fomitopsis pinicola. 115(62). BR: 2, 3, 4, 10, 13, 14, 21, 34, 41, 42. NB: 16, 23, 65, 69.
Heterobasidion annosum. 14(7). BR: 2, 10, 23, 42, 47, 50. NB: 3, 14, 68.
Rigidoporus lignosus. 1(0). NB: 5.
Rigidoporus nigrescens. 2(1). BR: 21. NB: 2.
Rigidoporus rigidus. 1(0). NB: 17.
Rigidoporus ulmarius. 6(1). BR: 69.
Rigidoporus vitreus. 2(1). BR: 69. NB: 21.
Rigidoporus zonalis. 1(0). NB: 5.
Antrodia sepium. 5(2). BR: 12, 34. NB: 47.
Antrodia serialis. 2(2). BR: 41.
Dichomitus squalens. 16(11). BR: 13, 47, 49. NB: 10.
Irpex tulipiferae. 3(1). BR: 69. NB: 2, 42.
Hirschioporus abietinus. 65(26). BR: 1, 18, 19, 30, 32, 61, 69. NB: 2, 74.
Hirschioporus pargamenus. 124(41). BR: 2, 10, 17, 18, 30, 32, 50, 69. NB: 10, 21, 42, 61, 63, 68, 74.
Hirschioporus sector. 16(9). BR: 8, 17, 32, 69.
Hirschioporus versatilis. 1(10). NB: 36.
Cerrena unicolor. 20(14). BR: 30, 42, 50, 54, 69.
Trametes cirrifer. 1(0). NB: 64.
Trametes plebeja. 4(0). NB: 5, 68, 69.
Trametes robiniophila. 3(1). BR: 27.
Pycnoporus cinnabarinus. 6(1). BR: 70. NB: 35, 37, 65, 69.
Pycnoporus sanguineus. 8(5). BR: 10, 55, 56. NB: 45, 63.
Coriolus biformis. 2(1). BR: 47. NB: 2.
Coriolus conchifer. 8(6). BR: 16, 74.
Coriolus hirsutus. 68(27). BR: 2, 7, 16, 26, 30, 31, 37, 64, 69, 70, 74. NB: 10, 35, 45, 58, 71.
Coriolus maximus. 11(8). BR: 35, 45, 55, 64. NB: 17.
Coriolus pinisitus. 15(7). BR: 45, 55. NB: 7, 17, 63.
Coriolus pubescens. 20(11). BR: 16, 26, 71, 74. NB: 21.
Coriolus subectypus. 4(3). BR: 9, 24, 45. NB: 16.
Coriolus tenuis. 1(0). NB: 45.
Coriolus versicolor. 417(211). BR: 2, 9, 16, 24, 26, 33, 35, 37, 38, 45, 46, 50, 69, 70, 71, 74. NB: 21, 44, 47, 54, 68.
Lenzites betulina. 66(28). BR: 16, 24, 35, 37, 38, 44, 45, 69, 70, 71, 74. NB: 21, 50.
Lenzites elegans. 16(9). BR: 35, 55, 69. NB: 10, 16, 17, 31.
Earliella corrugata. 12(7). BR: 5, 10, 17, 55, 64, 69. NB: 63.
Funalia hispida. 33(21). BR: 35, 37, 47, 50, 52, 69, 70. NB: 10, 68.
Funalia trogii. 1(1). BR: 69.
Coriolopsis crocata. 1(0). NB: 64.
Coriolopsis fulvocinerea. 8(4). BR: 11, 17, 63.
Coriolopsis occidentalis. 10(7). BR: 55, 64.
Gloeophyllum saepiarium. 4(3). BR: 47, 68.
Gloeophyllum striatum. 2(1). BR: 11. NB: 10.
Datronia mollis. 3(2). BR: 2. NB: 50.
Daedaleopsis confragosa. 5(4). BR: 2, 21, 47. NB: 68.
Pogonomyces hydnoides. 71(31). BR: 5, 6, 10, 11, 17, 51, 55, 58, 63, 64, 65. NB: 57, 62, 69, 72.
Fomes fomentarius. 24(12). BR: 21. NB: 2, 42, 63, 69, 72.
Fomes sclerodermeus. 23(8). BR: 10, 17, 57, 58, 69. NB: 51, 55, 65, 68.

Ganoderma applanatum. 152(75). BR: 2, 14, 21, 42, 50, 57, 65, 67, 68, 74. NB: 5, 10, 16, 17, 32, 34, 69, 70.
Ganoderma brownii. 14(11). BR: 14, 16, 50. NB: 37.
Ganoderma curtisii. 9(2). BR: 65, 68. NB: 28, 63, 69.
Ganoderma fulvellum. 1(1). BR: 10.
Ganoderma lobatum. 4(4). BR: 50, 65.
Ganoderma lucidum. 17(8). BR: 10, 17, 21, 28, 50, 69. NB: 57, 63.
Ganoderma oregonense. 3(2). BR: 13, 34. NB: 50.
Ganoderma tsugae. 21(8). BR: 2, 21, 69. NB: 36, 68.
Ganoderma zonatum. 23(15). BR: 17, 57, 62, 63, 65, 67. NB: 11.
Ganoderma spp. 15(7). BR: 17, 50, 67. NB: 52, 58, 63, 65, 68, 69.
Cyclomyces iodinus. 4(1). BR: 62. NB: 17, 28.
Inonotus corrosus. 3(3). BR: 6, 62, 72.
Inonotus munzii. 2(0). NB: 47.
Inonotus porrectus. 11(9). BR: 6, 62, 63.
Inonotus spp. 4(1). BR: 63. NB: 62, 68.
Phaeolus schweinitzii. 2(1). BR: 22.
Melanoporia nigra. (4(3). BR: 60, 62, 68.
Phellinus everhartii. 2(1). BR: 72.
Phellinus ferruginosus. 1(0). NB: 72.
Phellinus gilvus. 144(62). BR: 15, 59, 62, 63, 68, 72. NB: 10, 28, 32, 34, 36, 45, 50, 69, 70.
Phellinus igniarius. 17(9). BR: 68, 72. NB: 70.
Phellinus johnsonianus. 1(0). NB: 72.
Phellinus laevigatus. 4(3). BR: 72.
Phellinus licnoides. 13(8). BR: 62, 63. NB: 68, 72.
Phellinus pini. 2(2). BR: 22, 72.
Phellinus pomaceus. 1(0). NB: 72.
Phellinus ribis. 1(1). BR: 68.
Phellinus robiniae. 33(13). BR: 25, 53, 63, 68, 72. NB: 6, 21, 47.
Phellinus robustus. 4(2). BR: 72.
Phellinus spp. 4(4). BR: 15, 68, 72.

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